VOLUME LXXX NUMBER 3

THE
BOTANICAL GAZETTE

November 1925

PACIFIC COAST SPECIES OF LATHYRUS

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(WITH TWENTY-NINE FIGURES)

Since the publication of WHITE's revision of the North American species of *Lathyrus* in 1894, the species of the Pacific states have had no general treatment. A monograph of the entire genus, showing the relationships of the various species, is certainly needed; but the greatest need for such a work, on account of the confusion among the various species, seems to have existed for the Pacific states. Of the botanists since the time of WHITE, perhaps C. V. PIPER[1] has done the most toward restoring order, in so far as some species are concerned. That paper, however, did not include all the species, and several have been described since the revision, and extensive collections of material have been made; hence it seems desirable to prepare a more general revision of the species of the three coast states. This is only an attempt, however, since even at this date the region is in places botanically unknown, and an exposition of certain forms must as yet be undertaken with much hesitation. PIPER elucidated those subspecies related to *L. pauciflorus*. A similar treatment is needed for those allied to *L. splendens* and *L. Bolanderi*.

In some species, such as *L. Bolanderi*, the variation is so great that scores of forms might be described, but I cannot see the value of it at present. Further investigation will be necessary to determine their importance, which being done should be included in a detailed

[1] Proc. Biol. Soc. Wash. **31**: 189–197. 1918.

monograph. Accordingly no attempt has been made to name these numerous and perhaps inconstant variations, as, for example, the prostrate form with narrow leaflets and small stipules; the dwarfed erect form with dilated stipules and densely puberulent herbage; the form with broad, thin, glabrous leaflets and minute stipules; and the form with coriaceous leaflets and small stipules.

There is often a very noticeable variation in the leaflets, stipules, tendrils, color of the flowers, and appearance of the plant. This is due to ecological and other environmental conditions. There seems to be a tendency for plants with narrow leaflets to have small and narrow stipules, while in the same species those with broad leaflets have usually larger and more dilated stipules. Pubescence, while varying in many cases, is most often constant. The shape as well as the length of the calyx teeth is one of the most important and practically constant characters, and is of great diagnostic value in this genus, although it has never been given sufficient attention.

WHITE, in his key, overemphasized the importance of the length of the tendrils, and also the distinction between climbing and erect plants. It is true that species like *L. Cusickii* and *L. rigidus* are always erect; yet it is equally true that species like *L. Lanszwertii* and *L. pauciflorus* may be either erect or climbing. The climbing forms have well developed tendrils, while the erect ones have minute or no tendrils. Of the literature of the genus, preceding the work of WHITE,[2] can be mentioned that of ALEFELD[3] and that of WATSON.[4] In the last paper, which included all the then known species of North America, but thirteen were listed; WHITE's revision contained thirty-three.

Besides my own herbarium, I have had the use of specimens of the National Herbarium, University of California, Stanford University, University of Oregon, and the California Academy of Sciences. I am indebted to the curators of these herbaria, and also to J. C. NELSON, M. E. PECK, Miss MARY A. DAY, and the Director of the Royal Botanic Gardens at Kew for data, and to Dr. ABRAMS for assistance and advice. In the lists of specimens examined, the following abbreviations are used: RVB, my own herbarium; UO, Uni-

[2] Bull. Torr. Bot. Club **21**: 444–458. 1894.

[3] Bonplandia **9**: 146. 1861.

[4] Proc. Amer. Acad. **11**: 133–135. 1876.

versity of Oregon; UC, University of California; CA, California Academy of Sciences; DS, Dudley Herbarium of Stanford University; and US, United States National Herbarium.

LATHYRUS (Tourn.) L., Sp. Pl. 729. 1753.

Herbs climbing with well developed tendrils which terminate the leaves, or the tendrils much reduced and the plants erect; stipules foliaceous, as large as the leaflets or small and inconspicuous; leaves pinnate, with 2–20 leaflets, but with *L. aphaca* the leaflets are wanting, and the enlarged stipules assume the appearance of simple opposite leaves, the tendril projecting between them; flowers one to many in axillary racemes; calyx teeth 5, the 3 lower teeth usually longer than the 2 upper; corolla papilionaceous, campanulate at base; stamens diadelphous (9 and 1), monadelphous at base; ovary sessile or stalked; ovules usually numerous; style transversely flattened, curved and bent at right angles with ovary, dilated at summit and bearded on inner face for $\frac{1}{3}$–$\frac{1}{2}$ its length; pods flat or terete, 2-valved and 1-celled.

About 200 species, natives of South America and the northern hemispheres. Type species, *Lathyrus sativus* L.

KEY TO SPECIES AND SUBSPECIES

Leaflets 0–2; introduced species
- Leaflets 0; stipules large, resembling leaves; flowers yellow. 1. *L. aphaca*
- Leaflets 2; stipules and flowers otherwise
  - Plants annual; flowers small, pink or red
    - Pods hirsute; plants tall. . . . . 2. *L. hirsutus*
    - Pods glabrous; plants small and slender. . . . . 3. *L. sphaericus*
  - Plants perennial; flowers large, white or pink. . . . . 4. *L. latifolius*

Leaflets 2–20; native species
- Plants densely silky villous. . . . . 5. *L. littoralis*
- Plants not densely silky villous
  - Peduncle not longer than rachis of its leaf, or if so either the plants erect, less than a meter in height, or some of calyx teeth rather wide and longer than tube, or the flowers yellow; plants erect or climbing not over a meter high unless stems are winged or calyx teeth longer than calyx tube and about 2 mm. broad; flowers 10–25 mm. long
    - Calyx teeth usually shorter than calyx tube, or if longer either the plants with peduncles bearing one flower, or the teeth which exceed the tube very slender, not 2 mm. broad; flowers purple, blue, white,

or yellow; if yellow then the racemes with 2–7 flowers, or if as many as 11 flowers the stipules not one-half the size of leaflets
Flowers white or yellow
Leaflets narrowly lanceolate, much longer than wide
6. *L. Cusickii*
Leaflets oblong, lanceolate or obovate, 2–4 times as long as wide
Leaflets oblong or obovate, thin to coriaceous; stipules minute to one-half as large; flowers yellowish
Stipules minute
Flowers 10 mm. long; leaflets coriaceous....11. *L. Tracyi*
Flowers 20 mm. long; leaflets thin to coriaceous
10. *L. nevadensis*
Stipules $\frac{1}{3}$–$\frac{1}{2}$ size of leaflets.....10a. *L. nevadensis stipulaceus*
Leaflets oblong to linear, very veiny and coriaceous; stipules nearly as large; flowers white.....7. *L. rigidus*
Flowers purple or blue
Leaflets usually 4; stems not winged
Leaflets oval or oblong.....8. *L. bijugatus*
Leaflets narrowly linear.....8a. *L. bijugatus Sandbergii*
Leaflets 2–14; stems winged or without wings
Stipules small, except in 10a and 12, not one-half so large as adjacent leaflets
Stems not winged
Flowers 15–30 mm. long; leaflets about twice as long as wide; plants not villous
Flowers 15–16 mm. long, purplish to red; leaflets usually in 4 pairs
Leaflets elliptical.....9. *L. Nuttallii*
Leaflets lanceolate.....9a. *L. Nuttallii lanceolatus*
Flowers 20 mm. long, purplish to yellow; leaflets usually in 3 pairs
Stipules minute.....10. *L. nevadensis*
Stipules $\frac{1}{3}$–$\frac{1}{2}$ size of leaflets
10a. *L. nevadensis stipulaceus*
Flowers 15 mm. long or less; leaflets usually 3 or 4 times as long as wide, or else the plant villous and the flowers 1 or 2 in a raceme
Flowers usually 1.....12. *L. Torreyi*
Flowers more than 2
Plants tall; tendrils divided, sometimes well developed; leaflets various.....13. *L. Lanszwertii*
Plants low, erect; tendrils minute; leaflets linear
13a. *L. Lanszwertii aridus*

Stems winged; see nos. 17, 18, and 19
Stipules large, frequently one-half size of leaflets except in plants with narrow leaflets
Leaflets coriaceous, 6–12; flowers 3–5
Flowers 18–20 mm. long[5]
Leaflets broader than linear-lanceolate
Leaflets elliptic to ovate-lanceolate, acute
14. *L. pauciflorus*
Leaflets oval to ovate, obtuse
14a. *L. pauciflorus utahensis*
Leaflets linear to linear-lanceolate
14b. *L. pauciflorus tenuior*
Flowers 12–16 mm. long
Leaflets oval, elliptic or ovate
14c. *L. pauciflorus Schaffneri*
Leaflets linear to narrowly oblong
14d. *L. pauciflorus Brownii*
Leaflets flaccid, 10–20; flowers 6–10.....15. *L. polyphyllus*
Caiyx teeth usually longer than calyx tube, or, if shorter, the flowers yellow and borne 7–19 in the raceme and with dilated stipules, one-half size of leaflets; flowers white, purple, or blue; calyx teeth when long, rather broad, about 2 mm. wide
Flowers purplish to white or tawny
Stems not winged, or if so the leaflets not fleshy
Stems not winged
Stipules large, often one-half size of leaflets..16. *L. Bolanderi*
Stipules small or minute
Leaflets with white appressed hairs; flowers tawny
16a. *L. Bolanderi quercetorum*
Leaflets puberulent; flowers blue, white, or tawny
16b. *L. Bolanderi violaceus*
Stems frequently winged
Leaflets 8–12, pubescent or glabrous; flowers 6–15
Flowers rose purple, not fading to yellow; leaflets glabrous, somewhat glaucous.....17. *L. Jepsonii*
Flowers white, veined with purple, fading to yellow; leaflets puberulent to velvety pubescent
18. *L. Watsonii*
Leaflets 2–7, pubescent or glabrous; flowers 2–6
19. *L. palustris*
Stems never winged, leaflets fleshy.....20. *L. maritimus*

[5] This key to the subspecies of *L. pauciflorus* has been adapted from PIPER's paper.

Flowers yellowish
Leaflets thin, membranaceous.....21. *L. ochropetalus*
Leaflets thick, coriaceous.....22. *L. sulphureus*
Peduncle longer than rachis of its leaf; calyx teeth narrow, not so long as or scarcely exceeding the tube; plants several meters in length, climbing; flowers white, blue, or reddish, never yellow; flowers 20–35 or more mm. long; stems never winged
Flowers 3–3.5 cm. long, red or purple.....23. *L. splendens*
Flowers 2–2.5 cm. long, blue, purple, or white
Flowers white.....24. *L. lactiflorus*
Flowers not white.....24a. *L. lactiflorus Alefeldi*

1. LATHYRUS APHACA L., Sp. Pl. 729. 1753.—Annual, entirely glabrous; stems slender and climbing, 20–40 cm. high; stipules large, entire, broadly heart-shaped, resembling simple opposite leaves; leaflets none; tendrils well developed, about 2–3 cm. long, scarcely longer than stipules; peduncles slender, bearing 1 or 2 yellow flowers; flowers 6–9 mm. long; pods flat, 25 mm. long, containing 4–7 seeds.

This is one of the recently introduced species from Europe; it is well established along railroads and in gardens at Portland, Salem, and Eugene, Oregon. May–July. Type locality, "Habitat in Italia, Gallia, Anglia inter segetes." According to PARKER (Rhodora **23**:246. 1921), *L. nissolia* L. has been collected at Pullman, Washington. If found in the field it can readily be recognized by its pale red and rather small flowers, and leaves which are reduced to long, slender, flattened leaf stalks, without stipules. I have not examined a specimen from our limits.

OREGON.—Lane County: Eugene, May 1914, Mrs. *Norman*, Misses *Sanborn* and *Howell* (UO); same, May 1919, *Bradshaw* 1083 (RVB); same, May 18, 1919, *Bradshaw* (RVB); Multnomah County: Eastside, Portland, May 1919, *Nelson* 2592 (DS).

2. LATHYRUS HIRSUTUS L., Sp. Pl. 732. 1753.—Annual, the younger shoots somewhat hairy; stems branching at base, slender, 30 cm. or more high; margins of stems with prominent wings; stipules small and very narrow, hardly over 15 mm. long, linear-lanceolate; leaflets 2, linear-lanceolate, about 7 cm. long by 1 cm. wide; tendrils well developed, branching; peduncles longer than leaves, rather slender, bearing 1 or 2 small red flowers; flowers 7 mm. long; calyx teeth unequal, lower linear-lanceolate, upper deltoid, nearly as long as tube; pods flat, very hairy, about 4 cm. long; seeds 6–8.

This species was introduced at Salem, Oregon, on neglected parkings in 1919, where it has become well established. May. Type locality, "Habitat inter Angliae, Galliae segetes."

OREGON.—Marion County: Salem, July 1919, *Nelson* 2727 (DS).

3. LATHYRUS SPHAERICUS Retz., Obs. **3**:39. 1783.—Annual, perfectly glabrous; stems very slender, branching, 15–25 cm. high; stipules small, linear to subulate, 7–8 mm. long; leaflets 2, linear, 2–4 cm. long; tendrils represented only by short bristle; peduncles slender, 5–6 cm. long, bearing 1 small dark red flower; flowers about 8 mm. long; calyx teeth nearly equal in length, lowest linear-subulate, others linear, all longer than tube; pods 3–4 cm. long, glabrous; seeds 6–11.

This introduced annual has been collected at Salem, Oregon, where it was found on parkings. May. The type locality was not given with the original description.

OREGON.—Marion County: Salem, May 1919, *Nelson* 2534 (DS).

4. LATHYRUS LATIFOLIUS L., Sp. Pl. 733. 1753.—Perennial, perfectly glabrous; stems stout, climbing, very tall and coarse, petioles and stem broadly winged; stipules large and veiny, semi-sagittate, acute, sparingly serrate; leaflets 2, coriaceous, oblong-lanceolate, about 8 cm. long; tendrils as long as leaves, divided; peduncles sometimes 25 cm. long, of much greater length than leaves; flowers 6–10, pink or white, over 20 mm. long; calyx teeth glabrous, lowest subulate, upper triangular and very short; pods 5–8 cm. long.

This species is often planted in gardens, and is frequently met with as an escape in waste ground. Once established it is well able to hold its own. June–July. Type locality, "Habitat in Europae sepibus."

OREGON.—Lane County: Eugene, August 1920, *Bradshaw* 1953 (RVB); Marion County: Salem, June 1915, *Nelson* 270 (DS).

CALIFORNIA.—County not determined: Feather River region, June 1920, *Anna Head* (CA).

5. LATHYRUS LITTORALIS (Nutt.) Endl., Walp. Rep. **1**:722. 1842.—*Astrophia littoralis* Nutt. T. and G., Fl. N. A. **1**:278. 1838; *Orobus littoralis* Gray, Pacif. R.R. Rep. **4**:58. 1856.—Perennial, the entire plant densely silky villous; stems numerous, stout, decumbent, 15–65 cm. long; stipules more than twice the size of leaflets, ovate to oblong, entire; leaflets 2–10, linear-spatulate, 5–20 mm. long; tendrils none, leaf ending in small linear leaflet; peduncles

stout, 4–9 cm. long, greatly exceeding leaves; flowers 4–10, purple and white, about 20 mm. long; calyx teeth lanceolate, as long as tube, densely villous; pods 30 mm. long by 10 mm. broad, villous; seeds 3–5.—Fig. 10.

Along sea coasts, Humid Transition Zone, Washington, Oregon, and California. April–August. Type locality, "Sand hills of the estuary of the Oregon."

WASHINGTON.—Chehalis County: Laidlaw, May 1897, *Lamb* 1119 (DS); Island County: Whidby Island, *Gardner* (UC).

OREGON.—Clatsop County: Clatsop, August 3, 1887, *Henderson* 235 (DS); Clatsop Beach, July 1916, *Nelson* 819 (DS); Tillamook County: Tillamook Bay, July 1882, *Howell* (UO).

CALIFORNIA.—Humboldt County: Eureka, April 1918, *Paulson* (DS); Humboldt Bay, May 1906, *Tracy* 2451 (DS); Samoa, 1913, *Hutchinson* (CA); Marin County: Mt. Tamalpais, May 1891, *Cannon* (CA); Pt. Reyes, May 1906, *Eastwood* (CA); San Francisco County: Lake Merced, June 1887, *Greene* (DS, UC); near Cliff House, San Francisco, May 1902, *Baker* 695 (UC); Santa Cruz County: Watsonville, June 1903, *Elmer* 4390 (DS, CA); San Mateo County: Salida Beach, July 1918, *Brandegee* (UC); Halfmoon Bay, June 1905, *Brandegee* (UC).

6. LATHYRUS CUSICKII S. Wats., Proc. Amer. Acad. **17**:371. 1882.—Perennial, glabrous or slightly pubescent; stems slender, erect, branching, about 15–30 cm. high; stipules small, not half so long as adjacent leaflets, semi-sagittate, acuminate; leaflets 4–6, linear lanceolate to narrowly linear, 3–6 cm. long, acute or nearly so; tendrils none, sometimes a minute bristle present; peduncles slender, equaling or exceeding length of leaves, bearing 2 or 3 white flowers; flowers 20 mm. long; calyx teeth glabrous, linear, almost equal, not so long as tube; pods 4–5 cm. long by 6 mm. wide.—Fig. 17.

Dry mountain slopes, eastern Oregon; Canadian Zone. May-June. Type locality, "On dry mountain slopes, Union County, Oregon."

OREGON.—Eastern Oregon: dry forests, May 1882, *Cusick* (UC); Umatilla County: Blue Mountains, near Meacham, May 1908, *Cusick* 3236 (UO, DS); Union County: June 1882, *Cusick* 193 (UO, US); Imnaha National Forest: Chico Station, May 1907, *Coville* 2337 (US).

7. LATHYRUS RIGIDUS White, Bull. Torr. Bot. Club **21**:455. 1894.—*L. albus* S. Wats., Bot. Calif. **2**:442. 1880.—Perennial, glabrous and somewhat glaucous; stems stout, numerous from thick rootstalk, 20–30 cm. high; stipules nearly as large as leaflets, semi-sagittate, lanceolate, acuminate; leaflets 6–10, linear-oblong,

veiny and rigid like stipules, 1–2 cm. long, acute at both ends; tendrils none, a minute bristle terminating rachis of leaf; peduncles stout, equaling or exceeding leaves, bearing 2 or 3 flowers; flowers white, 15–20 mm. long; calyx teeth linear to deltoid, unequal, shorter than tube; pods glabrous, 3–3.5 cm. long by 7 mm. wide; seeds about 3.—Fig. 24.

Eastern Oregon, in the Blue Mountains to northern California; Arid Transition Zone. May–July. Type locality, Union County, Oregon.

OREGON.—Eastern Oregon, May 1897, *Cusick* 1604 (DS); Blue Mountains, May 1895, *Howell* (DS); Crook County: Willow Creek, June 1894, *Leiberg* 293 (DS, UO); Malheur County: May 1896, *Leiberg* 2117 (DS, UO, CA); Union County: April–May, 1910, *Cusick* 3428 (UO).

CALIFORNIA.—Modoc County: Goose Lake Valley, May 1894, Mrs. *Austin* (DS); Acabe Plains, 1894, Mrs. *Austin* 45 (UC); near Fort Bidwell, May 1904, Mrs. *Manning* 19 (UC); Davis Creek, June 1893, *Laura Black* 80 (DS).

8. LATHYRUS BIJUGATUS White, Bull. Torr. Bot. Club **21**:457. 1894.—Perfectly glabrous throughout; stems erect, rather slender, branching from base, 10–30 cm. high; stipules small, not half so large as adjacent leaflets, linear, subulate, semi-sagittate; leaflets about 4, oval to oblong or obovate, acute or obtuse, somewhat coriaceous, rather thin, paler beneath, 2–4 cm. long; tendrils very much reduced, represented by minute bristle; peduncles slender, half as long as leaves, bearing 2 or 3 purplish flowers; flowers 10 mm. long; calyx teeth nearly equal, triangular, about one-fourth as long as calyx tube; pods compressed; seeds about 6.—Fig. 15.

Eastern Washington and Idaho; Arid Transition Zone. May–June. Type locality, Latah County, Idaho.

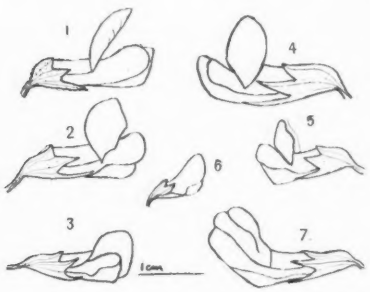
WASHINGTON.—Spokane County: Hangman Creek, May 1893, *Sandberg* and *Leiberg* 24 (US, UC, CA); Whitman County: Pullman, May 1897, *Elmer* 214 (US).

8a. LATHYRUS BIJUGATUS SANDBERGII White, Bull. Torr. Bot. Club **21**:457. 1894.—*L. Sandbergii* Howell, Fl. N.W.A. **1**:160. 1898.—This differs from the species in having narrowly linear or linear-lanceolate leaflets, 3–11 cm. long.

Eastern Washington and Idaho; Arid Transition Zone. May–June. Type locality, Latah County, Idaho.

WASHINGTON.—Whitman County: Pullman, May 1909, *Duthie* 15 (DS); same locality, June 1893, *Piper* (DS).

9. LATHYRUS NUTTALLII S. Wats., Proc. Amer. Acad. **21**:450. 1886.—*L. venosus* Muhl. var. σ T. and G., Fl. N.A. **1**:274. 1838.—Perennial, herbage sparingly pubescent throughout; stems rather slender, 40–90 cm. high, branching; stipules narrow, semi-sagittate, not half so long as adjacent leaflets, usually entire and long acuminate; leaflets 6–14, commonly 8, narrowly or broadly elliptical, acute, 2–5 cm. long; tendrils simple or divided, well developed but slender; peduncles slender, shorter or longer than leaves, bearing 4–6 reddish flowers; flowers 12–16 mm. long; calyx teeth unequal, not half so long as tube; pods oblong, glabrous, 25–40 mm. long; seeds several. —Fig. 3.



FIGS. 1–7.—Fig. 1, *L. Watsonii;* fig. 2, *L. palustris;* fig. 3, L. *Nuttallii;* fig. 4, *L. Jepsonii;* fig. 5, *L. Lanszwertii;* fig. 6, *L. Lanszwertii aridus;* fig. 7, *L. nevadensis.*

British Columbia to California in the coast region; Humid Transition Zone. May–July. Type locality, "Upper California."

This is somewhat similar to *L. nevadensis*, which is perhaps its nearest relative, but differs in the number of leaflets, and in the size and color of the flowers; *L. Nuttallii* has leaflets usually in 4 pairs, while *L. nevadensis* has leaflets generally in 3 pairs. The flowers of *L. Nuttallii* are reddish purple, while those of *L. nevadensis* are blue and white varying to yellow. *L. Nuttallii* is a taller plant and grows at a lower and more constant altitude.

WASHINGTON.—Chelan County: Chiwaukum, June 1904, *Whited* 2528 (UO); Clarke County: La Camas, June 1884, *Henderson* (DS); Kittitas County: Cle Elum, May 1897, *Whited* 364 (US); Klickitat County: Falcon Valley, April–August 1885, *Suksdorf* (UC); Pierce County: Tacoma, June 1920, *Eastwood* 9642 (CA); Skagit County: Weaverlings near Anacortes, May 1919, *Roush* (DS).

OREGON.—Sauvie's Island, May 1886, *Howell* 977 (UC); locality not determined: 1871, *Hall* (US); Lane County: Eugene, April 1920, *Bradshaw* 1364 (RVB); Multinomah County: Mt. Scott, May 1903, *Sheldon* 12012 (DS, UO).

CALIFORNIA.—Butte County: Stirling, May 1919, *Heller* 13162 (CA); Lake County: La Keport, May 1917, *Bentley* (DS); Siskiyou County: locality not given, July 1915, *Heller* 12091 (CA).

9a. LATHYRUS NUTTALLII LANCEOLATUS (Howell) Piper, Proc. Biol. Soc. Wash. **31**:191. 1918.—*L. lanceolatus* Howell, Fl. N. W. A.

1:158. 1898.—This subspecies has oblong-lanceolate leaflets of membranaceous texture and lanceolate stipules; the stipules are larger than with the species.

Oregon in the coast region; Humid Transition Zone. Type locality, Glendale, Oregon.

OREGON.—Sauvie's Island, May 1886, *Howell* (DS).

L. Peckii Piper (Proc. Biol. Soc. Wash. **31**:190. 1918) was based on only one specimen collected by M. E. PECK of Willamette University. PECK writes that only one specimen was found, and that on succeeding visits to the type locality (Harbor, Curry County, Oregon) no other plants could be obtained; accordingly the original was probably a hybrid or unusual growth of the variable *L. Nuttallii*.

10. LATHYRUS NEVADENSIS S. Wats., Proc. Amer. Acad. **11**:133. 1876.—*L. venosus obovatus* Torr., Pac. R. R. Rep. **4**:77. 1857, in part; *Vicia nana* Kell., Proc. Calif. Acad. **7**:89. 1876; *L. obovatus* White, Bull. Torr. Bot. Club **21**:455. 1894.—Perennial, glabrous to sparingly pubescent; stems erect, slender or stout, frequently branched, 10–45 cm. high; stipules small, not half so large as leaflets, semi-sagittate, linear-lanceolate, acute to acuminate; leaflets 4–8, ovate to ovate-oblong or obovate, acute or obtuse, usually rather thin but sometimes coriaceous, 0.5–3 cm. long, glabrous or slightly pubescent; tendrils represented usually by minute bristle, but larger specimens often have long and more developed simple tendrils; peduncles shorter or longer than leaves, bearing 2 or 3 bluish or ochroleucous flowers; flowers commonly 20 mm. or more long; calyx teeth linear to linear-lanceolate, not so long as tube; pods glabrous, 3 cm. long.—Fig. 7.

L. nevadensis is very variable; certain forms are small with coriaceous leaflets, while others more closely approach *L. Nuttallii*. There are forms similar to *L. Tracyi*, which has numerous small flowers 10 mm. long; but these forms are unlike *L. Tracyi* in the characters of stipules, leaflets, and general appearance. Between *L. nevadensis* and the subspecies *stipulaceus* are to be found specimens with stipules of varying sizes. One sheet examined, collected by *Rattan* in 1886 in El Dorado County, California, has both the large and the small stipules on plants collected evidently at the very same station. The specimen with the large stipules has more numerous flowers. Two other specimens collected by *Butler* (no. 1288) and *Heller* (no. 12007) may be at least of subspecific value. Both specimens have 7–10 yellowish flowers 10 mm. long. The stipules are well developed but not large, and the herbage is somewhat glaucous. Further study in the field is needed to determine whether they are distinct species or subspecies of *L. nevadensis*.

WASHINGTON.—Locality not given, 1889, *Vasey* 252 (US); Cascade Mountains near upper valley of Nesqually, July 1897, *Allen* 297 (DS).

OREGON.—Localities not determined: July 1886, *Cusick* 185 (UC); mountains in shade, *Cusick* (UO); Eastern Oregon: dry open forests, May 1898, *Cusick* 1881 (US); Wallowa Mountains, May, *Cusick* 2392 (DS); Southern Oregon: Grave Creek Mountains, May 1887 *Henderson* 1343 (DS, UO); southern slope of Siskiyous, June 1899, *Leiberg* 4039 (UO); Benton County: Corvallis, top of Mary's Peak, June 1916, *Gilbert* 109 (US); Coos County: south fork of Coos River, March 1911, *Smith* 3591 (US); Josephine County: Jones Creek, Grants Pass, April 1913, *Dale* (DS); Klamath County: Lake of the Woods, July 1897, *Coville* and *Applegate* 84 (US); Linn County: Smith River, July 1903, *Sheldon* 12738 (UO); Umatilla County: Blue Mountains, near Meacham, May 1908, *Cusick* (DS); same locality and date, *Cusick* 3336 (UO); Wasco County: Oregon National Forest, west of Friend, June 1917, *Lawrence* 282 (DS).

CALIFORNIA.—Amador County: Panther Creek, May 1895, *Hansen* 1084 (DS); Butte County: Forest Ranch, 1898, Mrs. *C. C. Bruce* 2082 (DS); Calaveras County: shade of big trees, May 1895, *Davy* 1547 (UC); Mokelumne Hill, F. E. Blaisdell (CA); Del Norte County: French Hill, April–May 1906, *Eastwood* 74 (CA); El Dorado County, locality not given, 1886, *Rattan* (DS); Glenn County: west of Bennet Spring, June 1915, *Heller* 12007 (CA); Humboldt County: Buck Mountain, June 1913, *Tracy* 4172 (UC); Klamath River, June 1901, *Chandler* 1443 (UC); Mariposa County: Sherlocks, May 1903, *Congdon* (UC); Sweetwater Peaks, May 1911, *Hall* 8842 (DS); Napa County: Howell Mountain, May 1902, *Tracy* 1527 (UC); Placer County: Dutch Flat, April 1921, *Patterson* (DS); Forest Hills, April 1865, *Bolander* 4629 (UC); Siskiyou County: Goosenest foothills, June 1910, *Butler* 1588 (DS); Humbug Mountain, May 1910, *Butler* 1288 (DS, UC); near Marble Mountain, June 1901, *Chandler* (UC); Tehama County: Mineral, July 1920, *Clemens* (CA); Trinity County: Trinity Summit, May–August 1899, *Davy* and *Blasdale* 5833 (UC); Yosemite: June 1911, *Hall* 8986; Yuba County: Camptonville, April 1918, *Eastwood* (CA).

10a. **Lathyrus nevadensis stipulaceus** (White), n. comb.—*L. obovatus stipulaceus* White, Bull. Torr. Bot. Club **21**:455. 1894.—This differs from the species in having enlarged stipules, one-third or one-half size of leaflets, and in having up to 10 flowers in the raceme.

With the species from British Columbia to California in the Transition Zone. The type locality for the species is "Mammoth Grove and Duffield's Ranch," Calaveras County, California. The subspecies was collected between Colville and Spokane, Washington.

CALIFORNIA.—El Dorado County: 1886, *Rattan* (DS), specimen marked "a."

11. **Lathyrus Tracyi,** n. sp.—Sparingly pubescent, bright green, not glaucous; stems erect, 58 cm. high, angled but not winged; stipules narrowly semi-sagittate, linear-lanceolate, subfalcate, not half so large as adjacent leaflets, entire or rarely dentate, acuminate at apex; leaflets coriaceous, veins of under surface puberulent, 3 or 4 pairs, 2–5 cm. long, 6–10 mm. wide, tapering from middle, acute at both ends; petioles 1 mm. long; tendrils of lower leaves minute, those of upper leaves divided, 15 mm. long; flowers 10 mm. long, yellow or cream colored, 10 or 11 in raceme; calyx teeth unequal, upper 1 mm. long, lateral linear-lanceolate, 2 mm. long, lowest 2.5 mm. long, none longer than calyx tube; fruit not seen.

Grouse Mountain, near Janes' Ranch, Humboldt County, California, May 26, 1918, *Tracy* 4943 (UC 202014, the specimen marked "a").

This species is related to *L. nevadensis* and *L. Lanszwertii*, having foliage and stipules like the latter, and flowers and general appearance suggesting the former.

12. LATHYRUS TORREYI Gray, Proc. Amer. Acad. **7**:337. 1867.—*L. Torreyi tenellus* Wiegand, Bull. Torr. Bot. Club **26**:135. 1899.—Perennial, minutely villous; stems slender, erect, branching, 15–45 cm. high; stipules small, 8–10 mm. long, usually not half so large as adjacent leaflets, lanceolate, acuminate, semi-sagittate; leaflets 8–14, rather thin, paler beneath, ovate to oblong or lanceolate, 5–10 mm. long, acute or obtuse; peduncles very slender, 8–40 mm. long, much shorter than leaves; flowers usually 1, sometimes 2, bluish white and about 10 or 15 mm. long; calyx teeth unequal, upper triangular, lower 3 subulate and longer than tube; pods scarcely over 25 mm. long, linear-oblong, somewhat pubescent; seeds 3–5.—Fig. 12.

In open woods, Washington, Oregon, to central California, in the coast region; Humid Transition Zone. April–July. Type locality, Mendocino or south part of Humboldt County, California.

WASHINGTON.—Pierce County: Tacoma, June 1894, *Thompson* (DS); same locality, June 1894, *Flett* (UO).

OREGON.—Southern Oregon: Siskiyou Mountains, July 1899, *Dudley* (DS); Clackamas County: Eagle Creek, June 1884, *Henderson* (DS); Lane County: Fall Creek, May 1920, *Wynd* (RVB); Marion County: Silver Falls, June 1916, *Nelson* 663 (DS).

CALIFORNIA.—Humboldt County: Willow Creek, June 1918, *Abrams* 7098 (DS); Dows Prairie, May 1917, *Tracy* 4786 (UC); Kneeland Prairie, August 1909,

Tracy 3062 (UC); Eureka, April 1913, *Hutchinson* (CA); Marin County: near Ross Valley, May 1904, *Baker* (UC); Bolinas Heights, June 1891, *Brandegee* (UC); Lagunitas Lake, May 1918, *Eastwood* (CA); Mendocino County: Lynal Ridge, June 1901, *Carruth* (CA); near Comtche, June 1906, *Walker* 271 (UC); near Orrs Hot Springs, May 1921, *Head* (CA); Walkirs Valley, Willets, May 1899, *Davy* and *Blasdale* 5099 (UC); Wolf Creek, July 1916, *Abrams* 5857 (DS); Napa County: St. Helena, Napa River, May 1897, *Jepson* (DS); near Calistoga; April 1894, *Jepson* (UC); Santa Clara County: near Gilroy, 1882, *Palache* (UC); Santa Cruz County: Big Basin, September 1901, *Dudley* (DS); by San Lorenzo road, May 1893, *Dudley* (DS); Sonoma County: Guerneville, May 1903, *Heller* 6614 (DS); Trinity County: between Mad and Trinity Rivers on Eureka–Red Bluff road, July 1916, *Abrams* 6199 (DS).

13. LATHYRUS LANSZWERTII Kellogg, Proc. Calif. Acad. **2**:150. 1863.—*L. palustris* S. Wats., Bot. King's Exp. 79. 1871; *L. coriaceus* White, Bull. Torr. Bot. Club **21**:452. 1894; *L. oregonensis* White, Bull. Torr. Bot. Club **21**:456. 1894, in part; *L. Goldsteinae* Eastw., Bull. Torr. Bot. Club **32**:197. 1905.—Perennial, herbage slightly puberulent throughout; stems stout and climbing, 20–45 cm. long, usually not branching; stipules slender, curved, lanceolate, long acuminate, semi-sagittate, sometimes one-half size of adjacent leaflets; leaflets 6–12, linear-lanceolate to elliptical, acute or obtuse, very firm and coriaceous, strongly venulose, 3–5 cm. long; tendrils well developed, commonly branching; peduncles rather slender, not so long as leaves, bearing 4–10 purplish white flowers; flowers 10–25 mm. long; calyx teeth unequal, shorter than tube; pods glabrous, 3–4 cm. long; seeds few.—Fig. 5.

Washington, Oregon, Nevada, California to Arizona; Upper Sonoran Zone. June–July. Type locality, Washoe, Nevada.

It seems evident[6] from a careful study of the original description of *L. Lanszwertii* and the illustration which accompanies it, that WHITE must have misunderstood this species, when he made it a synonym of *L. palustris* L. This is made even more evident when specimens from the type locality are examined. *L. Lanszwertii* represents the same sort of plant as *L. Goldsteinae*, which came from a similar region; both being practically the same as *L. coriaceus*, except that that is a form with somewhat wider leaflets.

WASHINGTON.—Chelan County: Lake Wenache, August 1893, *Leiberg* 634 (UO, CA, UC); Wenache Forest, Old Baldy Mountain, August 1916, *Eggleston* (US); Kittitas County: northeast Kittitas Valley, June 1903, *Cotton* 1208 (US); Yakima County: Yakima, June 18—, *Leckenby* (US).

[6] This was written before I had read HELLER's conclusion regarding the identity of *L. Lanszwertii* (Muhlenbergia **6**:92. 1910).

OREGON.—Baker County: Pine Creek and North Pine Creek, May 1886, *Cusick* 1372 (UO, US, UC); Pine Valley near Snake River, June 1898, *Cusick* 1918 (UO, UC); Crook County: Wolf Creek, Blue Mountains, July 1901, *Cusick* 2636 (UO, UC); Grant County: John Day River at Prairie City, July 1919, *Ferris* and *Duthie* 694 (DS); Harney County: near Mann Lake, June 1896, *Leiberg* 2404 (UO, UC); Steins Mountains, Divine Creek, July 1898, *Cusick* 1992a (UO, UC); Steins Mountains, July 1898, *Cusick* 1992 (DS, UO); Morrow County: 13.5 miles east of Heppener, July 1917, *Lawrence* 993 (DS).

CALIFORNIA.—El Dorado County: Fallen Leaf Lake, July 1906, *Thompson* (DS, US); Tallac, Lake Tahoe, July 1906, *Grant* (DS); Lakeside Park, Tallac, July 1908, *Brandegee* (UC); Tallac, July 1906, *Eastwood* 886 (CA); Camp Agassiz, July–August 1906, *Eastwood* 952 (CA); Plumas County: Quincy, July 1876, Mrs. *Austin* 29 (UC).

13a. **Lathyrus Lanszwertii aridus** (Piper), n. comb.—*L. oregonensis* White, Bull. Torr. Bot. Club **21**:456. 1894, in part; *L. graminifolius* of various authors, not Watson or White; *L. coriaceus aridus* Piper, Proc. Biol. Soc. Wash. **31**:190. 1918.—This subspecies has linear-lanceolate leaflets, 4–7 cm. long, and minute tendrils; flowers small, about 10 mm. long.—Fig. 6.

Washington, Oregon, and California; Upper Sonoran Zone. June–July. Type locality, "About Black Butte, Crook County, Oregon."

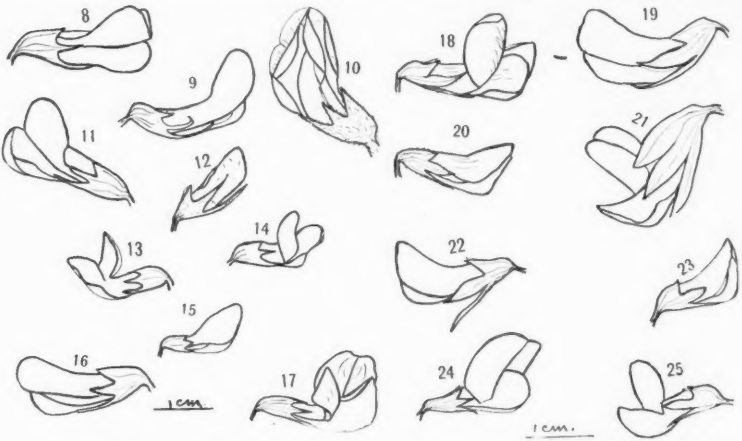
WASHINGTON.—Klickitat County: Falcon Valley, April 1885, *Suksdorf* (US).

OREGON.—Crook County: Black Butte, June 1902, *Cusick* 2814 (UO, DS, US); Farewell Bend, July 1894, *Leiberg* 433 (UC); Klamath County: near Lake of the Woods, July 1897, *Coville* and *Applegate* (US); Wasco County: White River, June 1881, *Howell* (DS); 3.5 miles west of Friend, June 1917, *Lawrence* 157 (DS).

CALIFORNIA.—Calaveras County: Bigtrees, Stanislaus Forest, June 1913, *Eggleston* 9212 (US); Plumas County: Quincy, June 1913, *Heller* 10851 (DS); Willow Creek, June 1912, *Hall* 9266 (UC); Tuolumne County: locality not given, June 1897, *Congdon* (UC); Yosemite, June 1911, *Hall* 8883 (DS).

14. LATHYRUS PAUCIFLORUS Fernald, Bot. Gaz. **19**:335. 1894.—*L. polyphyllus* S. Wats., Bot. King's Exp. 78. 1871; *L. ecirrhosus* Heller, Muhlenbergia **1**:54. 1904; *L. Bradfeldianus* A. Nels., Bot. Gaz. **54**:411. 1912.—Glabrous, frequently glaucous; stems stout, simple or branching, about 50 cm. high, climbing or erect; stipules large, usually half size of adjacent leaflets, broadly lanceolate, hastate; leaflets 6–12, elliptic to ovate-lanceolate, acute, usually firm and coriaceous, 1–4 cm. long; tendrils well developed or in certain

plants rather small and inconspicuous; peduncles either not so long as leaves or longer, bearing 3–8 purple flowers; flowers 18–20 mm. long; calyx glabrous, teeth unequal, upper triangular, 1–2 mm. long, lateral linear-lanceolate, scarcely as long as tube, and lowest linear, not exceeding tube; pods glabrous, 4 cm. long; seeds about 6.—Fig. 8.



FIGS. 8–25.—Fig. 8, *L. pauciflorus;* fig. 9, *L. pauciflorus utahensis;* fig. 10, *L. littoralis;* fig. 11, *L. pauciflorus tenuior;* fig. 12, *L. Torreyi;* fig. 13, *L. pauciflorus Brownii;* fig. 14, *L. pauciflorus Schaffneri;* fig. 15, *L. bijugatus;* fig. 16, *L. polyphyllus;* fig. 17, *L. Cusickii;* fig. 18, *L. Bolanderi violaceus;* fig. 19, *L. Bolanderi;* fig. 20, *L. Bolanderi quercetorum;* fig. 21, *L. maritimus;* fig. 22, *L. ochropetalus;* fig. 23, *L. sulphureus;* fig. 24, *L. rigidus;* fig. 25, *L. sulphureus.*

Washington, Oregon, Idaho, Wyoming, and California; Upper Sonoran and Arid Transition Zones. April–July. Type locality, Almota, Washington.

On the whole I agree with PIPER'S treatment of *L. pauciflorus* in "Some Western Species of *Lathyrus*," and so his key to the subspecies has been used. I do not think, however, that all the subspecies are of the same subspecific value; but not having had field experience with them, I am not able from the insufficient material examined to come to any further decisions. More field work is needed to determine the exact distribution of the species and subspecies. The species most closely allied to this group are found in the region dealt with in RYDBERG'S latest *Flora. L. pauciflorus* and its subspecies are similar in some respects to *L. Lanszwertii,* but the latter is nearly always furnished with puberulent herbage. *L. pauciflorus* is markedly glabrous and often glaucous. The stipules in the *L. pauciflorus* group are usually enlarged, unless the plants have narrow leaflets.

L. pauciflorus Brownii has often been confused with *L. graminifolius*, which apparently does not grow in California; at least I have seen no specimens. It is interesting to note here that *L. Lanszwertii aridus* has been mistaken for *L. graminifolius*. There is, it is true, a very superficial resemblance between *L. Lanszwertii aridus* and *L. pauciflorus Brownii*, and certain specimens collected by HELLER at Bennet Spring, Glenn County, California. seem to be somewhat intermediate between them.

L. pauciflorus has been confused with *L. polyphyllus*. One specimen collected by ALLEN in the upper valley of the Nesqually, in the Cascade Mountains, has a close resemblance to *L. polyphyllus*. *L. pauciflorus* has larger and fewer flowers; *L. polyphyllus* has more numerous leaflets, and they are never coriaceous. A specimen of *L. pauciflorus* with thin leaflets and numerous flowers suggests *L. polyphyllus* in general appearance, but the individual flowers are always different, the calyx teeth of the latter being ciliate.

There seems to be no apparent difference between *L. ecirrhosus* and *L. pauciflorus*.

WASHINGTON.—County not determined: upper valley of the Nesqually, Cascade Mountains, June–July 1895, *Allen* 132 (US, DS); Chelan County: between Drury and Chiwaukum, May 1920, *Otis* 889 (US); Hoose Lake region, near Wenache, May 1899, *Whited* 1106 (DS); hills across river from Leavensworth, May 1918, *Otis* 681 (CA); Klickitat County: hillsides near Columbia River, April–June 1886, *Suksdorf* 854 (US); Whitman County: Almota, June 1894, *Piper* (UC).

OREGON.—Counties not determined: Blue Mountains, May 1885, *Howell* (US); eastern Oregon, June 1881, *Howell* (UO); Clackamas County: Oswego, May 1891, *Gorman* (UO); Wallowa County: Fence Creek, no date, *Cusick* (UO); Lost Prairie, June 1900 (UO).

CALIFORNIA.—Lake County: Mt. Sanhedrin, July 1902, *Heller* 5944 (DS); Nevada County: Sugar Loaf Hill, Nevada City, June 1893, *Dudley* (DS); Plumas County: near Quincy, June 1913, *Heller* 10833 (DS); Sutter County: north side of Marysville Buttes, May 1914, *Heller* 11370a (DS).

14a. LATHYRUS PAUCIFLORUS UTAHENSIS (Jones) Piper, Proc. Biol. Soc. Wash. **31**:194. 1918.—*L. utahensis* Jones, Proc. Calif. Acad. Sci. N. S. **2**:678. 1895.—Distinguished from the species by the obtuse, oval to ovate leaflets.—Fig. 9.

Washington, Oregon, Utah, Colorado, and Arizona; Upper Sonoran and Arid Transition Zones. April–July. Type locality, "Ireland's Ranch, Utah, at the head of Salina Canyon."

OREGON.—Counties and localities not determined: 1884, *Cusick* (US 42779); *Cusick* (UO 1756. 1); Baker County: mountains near North Pine Creek, May 1901, *Cusick* 2538 (US, UO); Union County: locality not given, 1884, *Cusick* 756 (US).

14b. LATHYRUS PAUCIFLORUS TENUIOR Piper, Contrib. U.S. Nat. Herb. **11**:378. 1906.—*L. parvifolius tenuior* Piper, Fl. Palouse Reg. 108. 1901; *L. tenuior* Rydb., Fl. Rocky Mts. 528. 1917.—This subspecies has linear-lanceolate leaflets, 3–6 cm. long.—Fig. 11.

Eastern Washington and Idaho; Arid Transition Zone. May–June. Type locality, "Snake River bluffs near Almota," Washington.

WASHINGTON.—Whitman County: Almota, 1896, *Elmer* 52 (US).

OREGON.—Morrow County: near Rock Creek, May 1894, *Leiberg* 77 (UC); Ochoco Nat. Forest, May 1912, *Ingram* (US); Wallowa County; locality not given, June 1900, *Cusick* 2408 (US).

14c. LATHYRUS PAUCIFLORUS SCHAFFNERI Piper, Proc. Biol. Soc. Wash. **31**:194. 1918.—*L. parvifolius* S. Wats., Proc. Amer. Acad. **17**:345. 1882; *L. Schaffneri* Rydb., Mem. N.Y. Bot. Gard. **1**:258. 1900.—This subspecies has flowers 12–16 mm. long, and oval, elliptic, or ovate leaflets; the tendrils are either well developed or minute.—Fig. 14.

Mexico, Arizona, New Mexico, Colorado, California, and Lower California; Upper Sonoran and Arid Transition Zones. April–July. Type locality, San Miguelito Mts., San Luis Potosi, Mexico.

CALIFORNIA.—County not determined: Sierra Nevada Mts., 1875, *Lemmon* (US); Butte County: Los Vergils, April 1920, *Kelley* (CA); Kern County: Water Canyon, Techachapi Mts., June 1908, *Abrams* and *McGregor* 443 (DS); Modoc County: locality not given, June 1893, *Baker* (UC); Forestdale, 1893, *Baker* (UC); near Parker Creek, June 1919, *Ferris* and *Duthie* 124 (DS); Plumas County: Massack Creek, May 1919, *Wagner* 258b (DS); Big Meadows, July 1878, Mrs. *Austin* 39 (UC); Portola, May 1918, *Eastwood* 7029 (CA); Sierra County: Sierra Valley, *Lemmon* (DS); Siskiyou County: locality not determined, April 1910, *Butler* 1212 (DS).

14d. LATHYRUS PAUCIFLORUS BROWNII (Eastw.) Piper, Proc. Biol. Soc. Wash. **31**:195. 1918.—*L. Brownii* Eastw., Bull. Torr. Bot. Club **30**:491. 1903; *L. graminifolius* of various botanists, not Watson or White.—This subspecies has flowers about 10 mm. long, and linear or linear-lanceolate leaflets; the tendrils are frequently minute or absent.—Fig. 13.

Oregon, California, and Arizona; Arid Transition and Upper Sonoran Zones. May–July. Type locality, "North side of Mount Shasta."

OREGON.—Klamath County: June 1896, *Applegate* 147 (US).

CALIFORNIA.—Glenn County: west of Bennet Spring, June 1915, *Heller* 12006; this is somewhat unlike typical *L. pauciflorus Brownii* (CA); Kern

County: Water Canyon, Techachapi Mts., June 1908, *Abrams* and *McGregor* 443 (US, DS. Some of the sheets with this number have specimens of *L. pauciflorus Brownii*, while others have *L. pauciflorus Schaffneri* and variations between the two); Lassen County: Susanville, July 1892, *Brandegee* (UC); Nevada County: Castle Crag trail, June 1893, *Dudley* (DS); Plumas County: Massack Creek, May 1919, *Wagner* 258a (DS); Prattville, summer 1906, Mrs. *Coombs* (CA); Shasta County: Burney, June 1912, *Eastwood* (CA); Castilla, May 1904, *Piper* 6367 (US); Sierra County: Portola, May 1918, *Eastwood* (CA); Siskiyou County: Weed, May 1913, *Smith* 272 (CA. Flowers large, suggesting the subspecies *tenuior*); north side of Mount Shasta, June 1897, *Brown* (US. Duplicate type); Mt. Eddy, July 1915, *Heller* 12096 (DS); Greenhorn Mountain, May 1910, *Butler* 1346 (DS); Tehama County: Red Bluff, June 1917, *Wicks* (CA).

15. LATHYRUS POLYPHYLLUS Nutt. T. and G., Fl. N.A. 1:274. 1838.—Perennial, glabrous throughout; stems erect or nearly so, climbing, stout and angled, 70–100 cm. high; stipules as large as adjacent leaflets, semicordate, frequently dentate; leaflets 10–20, distinctly petiolulate, paler beneath, somewhat flaccid, oblong, acute or obtuse, 2–4 cm. long; tendrils well developed; peduncles slender, not so long as leaves; flowers 6–10, purple, 15–20 mm. long; calyx teeth ciliate, upper 2 triangular, others subulate, as long as tube; pods linear-oblong, glabrous, 5 cm. long; seeds 2–10.—Fig. 16.

Common in open coniferous woods from British Columbia to northern California; Humid Transition Zone. May–August. Type locality, "Forests of the Oregon toward the sea."

WASHINGTON.—Clallam County: Olympic Mountains, August 1900, *Elmer* 2535 (DS); King County: Mercer Island, Seattle, June 1920, *Eastwood* 9956 (CA); Klickitat County: locality not given, May 1891, *Suksdorf* 2021 (DS); Pierce County: Tacoma, June 1920, *Eastwood* 9642 (CA).

OREGON.—Douglas County: Rogue River, near Elk Creek, July 1899, *Leiberg* (UO); Lane County: Eugene, May 1920, *Bradshaw* 1555 (RVB); Marion County: Salem, April 1915, *Nelson* 69 (DS); Multnomah County: Rocky Butte, May 1903, *Sheldon* 12032 (DS, UO); Portland, May–June 1883, *Henderson* (DS, UO).

CALIFORNIA.—North Coast Ranges: Bell Springs to Harrison, May–August 1899, *Davy* and *Blasdale* 5355 (DS, UC); data not given: State Survey 4685 (UC); Humboldt County: Valley of Van Duzen River, opposite Buck Mt., June–July 1908, *Tracy* 2731 (UC); Little Bear Harbor, Geol. Surv. Calif. 6508, *Bolander* (UC); Mendocino County: Idol House, May 1901, *Chandler* 1075 (UC); Sherwood, May 1899, *Davy* and *Blasdale* 1068 (UC); Trinity County: Trinity Summit, July 1901, Mrs. *Manning* 62½ (UC).

16. LATHYRUS BOLANDERI S. Wats., Proc. Amer. Acad. **20**:363. 1885.—Stems stout, up to meter in height, herbage glabrous or puberulent, perennial; stipules half as large as adjacent leaflets, dilated, semi-sagittate, often toothed; leaflets 6–10, lanceolate to broadly ovate, acute or obtuse, usually thin but sometimes coriaceous, 25–50 mm. long; tendrils stout, well developed and branching; peduncles equaling or exceeding leaves, bearing 8–10 flowers, from blue to white or pink in color, each about 20 mm. long; calyx teeth unequal, upper 2 about 2 mm. long, lateral linear-lanceolate 8 mm. long, lowest linear often 10 mm. long, and frequently twice the length of calyx tube; pods glabrous, 5–6 cm. long; seeds 3–6.—Fig. 19.

Southern Oregon to southern California along the coast; Humid Transition and Upper Sonoran Zones. March–June. Type locality, "Oakland Hills near San Francisco."

This is one of the most abundant species on the western or seaward slope of California. Its most striking features are its enlarged stipules and broad, elongated calyx teeth. The pubescence is very variable. The difference between this species and what has been known as *L. violaceus* or *L. vestitus puberulus* is very slight. The essential characters are the same, such as the characteristic calyx teeth and the general habit. As has been mentioned before, the stipules and leaflets are extremely inconstant in shape and size. At best I should consider *L. quercetorum* but a subspecies of *L. Bolanderi*. The latter often has tawny flowers. The pubescence of the former is probably its best and most pronounced character. What the original *L. vestitus* was, which NUTTALL collected from the "Columbia plains toward the sea," no botanist has been able to determine. Possibly it was something similar to *L. Bolanderi*, or *L. Bolanderi violaceus*. It apparently has never been collected by any one since that time.

OREGON.—Douglas County: Glendale, June 1902, *Jones* (US).

CALIFORNIA.[7]—Alameda County: Point Isabel, West Berkeley, April 1897, *Davy* (UC); Contra Costa County; Fish Ranch, *Jepson* (UC); Del Norte County: Smith River, April 1902, *Goddard* 328 (UC); Humboldt County: Willow Creek, June 1918, *Abrams* (DS); Marin County: Mt. Tamalpais, November 1914, *Eastwood* (CA); Mendocino County: Kaisen District, June 1903, *McMurphy* 132 (DS); Monterey County: between Pebble Beach and Carmel, March 1910, *Randall* 167 (DS); Napa County: Mt. St. Helena, March 1907, collector not given (CA); San Francisco County: south end of Lake Merced, May 1901, *Dudley* (DS); San Mateo County: Crystal Lake, April 1902, *Abrams* 2342 (DS); Sonoma County: Duncan's Mills, July 1882, *Jones* 3576 (CA); Ventura County: San Buenaventura, Geol. Survey, March 1861, *Brewer* 236 (US).

[7] Space does not permit a citation of all the specimens examined of the species and the subspecies *violaceus*.

16a. **Lathyrus Bolanderi quercetorum** (Heller), n. comb.—*L. quercetorum* Heller, Muhlenbergia **2**:290. 1907.—This subspecies is more dwarfed than the species; the leaflets are covered with appressed white hairs; the flowers are tawny, and the calyx teeth not so long as with the species, but are similar in shape.—Fig. 20.

Mt. Hamilton and Mt. Diablo, California; Upper Sonoran Zone. April. Type locality, "Near the summit of Mt. Hamilton, Santa Clara County," California.

CALIFORNIA.—Napa County: Mt. Diablo, April 1862, State Survey (UC); Santa Clara County: Mt. Day in the Hamilton Range, April 1908, *Heller* 8926 (DS); Mt. Hamilton, May 1907, *Heller* 8623 (DS); same locality, 1891, *Greene* (UC).

16b. **Lathyrus Bolanderi violaceus** (Greene), n. comb.—*L. violaceus* Greene, Erythea **1**:105. 1893; *L. puberulus* White; Greene, Man. 85. 1894; *L. vestitus puberulus* Jepson, Fl. W. Mid. Cal. **1**: 298. 1901.—This subspecies is more puberulent than the species; the stipules more narrow, smaller, and the flowers less numerous; the leaves are often darker, more coriaceous, and the stems longer and more branched, and more frequently found climbing over bushes than the smaller more succulent typical *L. Bolanderi;* somewhat more like *L. Bolanderi quercetorum*, although all sorts of variations occur.—Fig. 18.

Northern to southern California in the coast region; Upper Sonoran and Humid Transition Zones. March–June, often flowering in the late fall or winter. Type locality, type specimens grown at the University of California from seeds collected in the mountains of Los Angeles County, California.

WHITE'S *L. violaceus barberae* from the description seems to be one of the many variations of *L. Bolanderi*. These leaflet variations are anything but constant; however, I have seen no material so designated by WHITE. He described the calyx thus: "upper calyx teeth exceeding the tube, lateral ones broader and about the length of the tube, the lowest broad and much shorter." Part of this must be a misprint, for "upper calyx teeth exceeding the tube" is certainly very far from true with any of the plants related to *L. Bolanderi*, although the statement regarding the lateral teeth agrees with most of the material of *L. Bolanderi* and its allies. It is interesting to note that in the material examined in the various herbaria, nearly all the collectors have used the name *L. violaceus barberae* for forms of *L. laetiflorus Alefeldi* with narrow leaflets. It is clear, however, that the description of the form in question suggests *L. violaceus* of GREENE, rather than any of the species related to *L. splendens*, which never have broad or greatly elongated calyx teeth.

WHITE considered that *L. strictus* Nuttall (not *L. strictus* Grauer, 1784) might have been either *L. violaceus* or *L. violaceus barberae*, or even both. This may be true, but the possibility is that NUTTALL'S *strictus* was a form of *L. laetiflorus Alefeldi* with very narrow leaflets, for all those allied to *L. splendens* have occasionally narrow leaflets, especially in the upper part of the plant.

The following specimens are referred to *L. Bolanderi violaceus*.

CALIFORNIA.—Alameda County: Oakland, May 1887, *Rattan* (DS); U. of C. Botanic Gardens, 1893, *Davy* (UC. From the type); Contra Costa County: Camp 69, Walnut Creek, April 1862, *Brewer* 1018 (UC); Lake County: Sulphur Banks, April 1902, *Bowman* 168 (DS); Los Angeles County: Santa Monica Mts., April 1901, *Abrams* (DS); Marin County: Corte Madera, March 1903, *Sheldon* 11564 (UO); Monterey County: Pacific Grove, April 1909, *Abrams* 4208 (DS); Napa County: St. Helena, July 1891, *Greene* (UC); Santa Barbara County: Santa Inez River, May 1907, *Hall* 7826 (UC); Santa Clara County: foothills west of Los Gatos, April 1904, *Heller* 7283 (DS); Santa Cruz County: Santa Cruz, June 1903, *Thompson* (DS); San Francisco County: Lake Merced, May 1918, *Eastwood* (CA); San Luis Obispo County: San Luis Obispo, spring 1905, *Roadhouse* 87 (UC); San Mateo County: Crystal Springs Lake, May 1922, *Bradshaw* 2752 (RVB); Sonoma County: near Sonoma, April 1862, *Brewer* 966 (UC); Ventura County: Saticoy, April 1916, *Eastwood* 5049 (CA).

17. LATHYRUS JEPSONII Greene, Pittonia **2**:158. 1890.—*L. palustris* L. var. ϵ T. and G., Fl. N.A. **1**:276. 1838.—Perennial, nearly glabrous; stems with prominent wings, 1.5–3 m. high, rather stout; stipules much smaller than adjacent leaflets, semi-sagittate, acuminate, entire or toothed; leaflets 8–12, linear-lanceolate, acute, usually firm and coriaceous, veins very pronounced, 3–5 cm. long; tendrils well developed, commonly divided; peduncles stout, 15–30 cm. long, about equaling leaves; flowers 6–15, usually 20 mm. long, rose-purple, becoming darker upon fading and drying; calyx teeth unequal, 2 upper very short, other 3 about as long as tube; pods glabrous, 7 cm. long, compressed; seeds 12–16.—Fig. 4.

Tidewater sloughs at Suisun, California, also at Stockton; Upper Sonoran Zone. August–September. Type locality, "Suisun marshes, also toward Stockton."

L. Jepsonii is a very local species, doubtless closely allied to *L. Watsonii*, and both suggest relationship with certain forms of *L. Bolanderi* rather than with *L. palustris* L. This is shown by the large flowers of *L. Jepsonii* and *L. Watsonii*, as well as by the size and shape of the calyx teeth. The calyx teeth of *L. Jepsonii* and *L. Watsonii* are nearly always shorter than those of *L. Bolanderi;* but although the calyx teeth are shorter, they are in both cases of similar shape. If *L. palustris* is related to any of the American species of *Lathyrus*, it is probably

closest to *L. Lanszwertii*, but the relationship is distant, for *L. palustris* is distinct. While *L. palustris* and *L. Jepsonii* are most commonly found near water, *L. Watsonii* is frequently collected in drier habitats.

The following specimens are referred to *L. Jepsonii*.

CALIFORNIA.—Napa County: tidal marsh in Napa River, August 1892, *Bioletti* (DS); Drawbridge, August 1892, *Bioletti* (UC); San Joaquin County: Stockton, 1903, *Berg* (DS); Rough and Ready Island, November–December 1903, *Berg* (UC); Solano County: Suisun Marshes, October 1905, *Dudley* (DS); same locality, June 1903, *Baker* 3226 (US, DS); same locality, August 1903, *Baker* (US); same locality, August 1920, *Jones* (CA); same locality, July 1913, *Eastwood* 3445 (CA).

18. LATHYRUS WATSONII White, Bull. Torr. Bot. Club **21**:447. 1894.—*L. venosus californicus* S. Wats., Proc. Amer. Acad. **11**:133. 1876; *L. californicus* S. Wats., Proc. Amer. Acad. **20**:363. 1885.—Perennial, puberulent to velvety pubescent; stems ordinarily with prominent wings, 1–2 meters high, rather stout and frequently branching; stipules not half so large as the adjacent leaflets, semi-sagittate, dilated, commonly toothed at base, long acuminate; leaflets 8–12, ovate to linear-lanceolate, obtuse or acute, very firm and coriaceous, strongly venulose, 1–5 cm. long; tendrils well developed, divided; peduncles stout, 10–25 cm. long, not exceeding leaves, bearing 6–15 flowers; flowers about 20 mm. long, white veined with pink or purple, fading to deep yellow; calyx teeth unequal, upper 2 very short, 3 lowest scarcely exceeding tube; pods glabrous, 5–6 cm. long; seeds 4–6.—Fig. 1.

California as far south as Monterey County; Upper Sonoran and Arid Transition Zones. April–July. Type locality, Monterey and Sonoma Counties.

CALIFORNIA.[8]—Alameda County: Alameda, May 1891, *Greene* (DS); Amador County: Panther Creek, 1895, *Hansen* 1299 (DS); Butte County: Berry Canyon, near Clear Creek, May 1902, *Heller* and *Brown* 5489 (DS); Calaveras County: Murphy's Camp, May 1895, *Davy* 1492 (UC); Contra Costa County: Alhambra Valley, May 1887, *Rattan* (DS); El Dorado County: Pyramid Peak, 1900, *Atkinson* (DS); Fresno County: Toll House, June 1900, *Hall* and *Chandler* 37 (UC); Humboldt County: Dinsmore's Ranch, valley of Van Duzen River, June 1913, *Tracy* 4110 (UC); Kern County: Bisse's Station, June 1895, *Dudley* 485 (DS); Lake County: Mt. Sanhedrin, July 1913, *Hall* 9494 (UC); Marin County: White's Hill, August 1920, *Eastwood* 10016 (CA); Mariposa County: locality not given, April 1915, *Eastwood* 4359 (CA); Mendocino County: Sherwood Valley, June 1899, *Dudley* (DS); Monterey County:

[8] A greatly abbreviated list of specimens examined.

Castroville, May–June 1901, *Davy* 7546 (DS, UC); Napa County: along Napa River near Ritherford, May 1904, *Tracy* 2079 (UC); Placer County: Emigrant Gap, July 1882, *Jones* 3573 (CA); Plumas County: thickets along streams, July 1900, *Leiberg* 5180 (UO); San Benito County: Hernandez, June 1903; *Lathrop* (DS); Santa Clara County: foothills near Stanford University, May 1902, *Baker* 849 (CA, UC); Santa Cruz County: locality not given, June 1914, *Smith* 2891 (CA); San Mateo County: Crystal Spring's Lake, May 1922, *Bradshaw* 2753 (RVB); San Luis Obispo County: Paso Robles, May 1899, *Barber* (UC); Shasta County: Redding, May 1913, *Smith* 238 (CA); Sierra Nat. Forest: July 1912, *Abrams* 4979 (DS); Sierra County: Cedar Glen, May 1920, *Jones* (CA); Siskiyou County: by Sacramento River, August 1905, *Dudley* (DS); Solano County: Elmira, May 1903, *Baker* 2922 (UC, CA); Sonoma County: Santa Rosa Creek, east of Santa Rosa, June 1902, *Heller* 5659 (DS); Trinity County: Coffee Creek, Salmon Mts., July 1909, *Hall* 8527 (UC); Tulare County: Kaweah River, 18 miles east of Visalia, March 1898, *Woolsey* (UC).

19. LATHYRUS PALUSTRIS L., Sp. Pl. 733. 1753.—*L. occidentalis* Nutt.; T. and G., Fl. **1**:276. 1838, as a synonym.—Perennial, glabrous or pubescent; stems slender, climbing, about 60 cm. high, wings often as broad as stem; stipules small or sometimes one-third size of adjacent leaflets, narrow, acuminate, semi-sagittate; leaflets 4–6 (or rarely 2), firm, acute or obtuse, linear to oblong, 2–5 cm. long; tendrils well developed; peduncles longer than leaves, bearing 2–6 purple flowers; flowers 10–30 mm. long; calyx teeth very unequal, 2 upper scarcely more than 1–2 mm. long, 3 lower nearly as long as tube; pods glabrous, linear oblong, 5 cm. long; seeds 6–8.—Fig. 2.

In marshes especially along the seashore; Humid Transition Zone; Alaska to northern California, New England, and Europe. May–August. Type locality, "In Europe borealis pascuis paludosis."

OREGON.—Clatsop County: Waluski River, August 1902, *Sheldon* 10220 (DS, UO); Douglas County: mouth of Umpqua River, June 1885, *Howell* (DS); Lincoln County: Newport, July 1919, *Bradshaw* 712 (RVB); 9 miles south of Newport, June 1918, *Lawrence* 1783 (US).

CALIFORNIA.—Butte County: De Sabla, June 1917, *Edwards* (DS 81643, UO. Flowers large; leaflets 2); Del Norte County: Lake Earle, June 1902, *Davy* (UC); Humboldt County: near Samoa, July 1907, *Tracy* 2593 (DS, UC); Mendocino County: barrens back of Mendocino, June 1903, *McMurphy* 473 (DS).

20. LATHYRUS MARITIMUS (L.) Bigel., Fl. Bost. ed. **2**. 268. 1824.—*Pisum maritimum* L., Sp. Pl. 727. 1753; *L. californicus* Dougl.; Lindl., Bot. Reg. *pl. 1144.* 1828; *L. pisiformis* Hook., Fl.

Bor. Am. 1:158. 1834.—Perennial, glabrous, slightly glaucous; stems stout, decumbent, 25–90 cm. long; stipules large, about half size of adjacent leaflets, ovate, acute, entire or lower lobe dentate; leaflets 8–12, pale and rather fleshy, nearly sessile, oblong to ovate, acute or obtuse, 1–5 cm. long; tendrils well developed; peduncles about length of leaves; flowers 6–10, purple and white, nearly 20 mm. long; calyx teeth unequal, 2 upper as long as tube, 3 lower longer than tube; pods flat, slightly pubescent, 5–6 cm. long; seeds about 10.—Fig. 21.

Along sea coasts, Alaska to California, shores of Great Lakes, Labrador to New Jersey, and northern Europe and Asia; Humid Transition Zone. May–August. Type locality, "Habitat in Europae borealis littoribus maris arenosis."

WASHINGTON.—Camano Island, June 1896, *Gardner* (UC.); Chehalis County: near South Arbor, May 1897, *Lamb* 1112 (DS); Clallan County: Olympic Mts., near coast, *Elmer* 2528 (DS); La Push, June 1921, *Taylor* (CA); King County: Fort Lawton, Seattle, June 1920, *Eastwood* 9621 (CA); Pacific County: Ilwaco, July 1886, *Henderson* (DS, UO); San Juan County: Brown's Island, Friday Harbor, July 1904, *Berg* 61 (DS); False Bay, San Juan Island, June 1919, *Roush* (DS).

OREGON.—Clatsop County: Clatsop Beach, July 1916, *Nelson* 822 (DS); Lincoln County: Newport, July 1919, *Bradshaw* 713 (RVB).

CALIFORNIA.—Del Norte County: near Crescent City, October 1909, *Tracy* 3107 (UC); Humboldt County: Eureka, Humboldt Bay, July 1912, *Tracy* 3736 (UC).

21. LATHYRUS OCHROPETALUS Piper, Proc. Biol. Soc. Wash. 31: 189. 1918.—Perennial, perfectly glabrous throughout and somewhat glaucous; stems climbing, slender, about 1–2 m. high; stipules large, half size of adjacent leaflets, ovate, nearly entire; leaflets 4–10, ovate to ovate-lanceolate, acute, membranaceous, paler beneath, 3–6 cm. long; tendrils well developed, branching; peduncles rather stout, about half length of leaves; flowers 7–13, pale yellow, 20 mm. long; calyx teeth unequal, 2 upper triangular, scarcely over 1 mm. long, lateral oblong-lanceolate, as long as tube, ventral slightly exceeding tube; pods glabrous, 4 cm. long; seeds about 6.—Fig. 22.

Western Washington and Oregon; Humid Transition Zone. May–June. Type locality, Seattle, Washington.

More field work will be required in order to determine the exact relationship and position of *L. ochropetalus*. From the material examined, it seems to be intermediate between *L. Bolanderi* and *L. sulphureus*, and suggests also a con-

nection with *L. polyphyllus*, especially in the shape of the leaflets and the peculiarity of the foliage. This species may prove to be only a northern form of *L. Bolanderi*, however, the floral characters of these being very similar, particularly the calyx teeth. *L. sulphureus* always has smaller flowers. In the herbaria *L. ochropetalus* has passed for both *L. sulphureus* and *L. polyphyllus*. Much that goes by the name of *L. sulphureus* is really only a yellow flowered form of *L. Bolanderi*. The distribution of these is very different. *L. Bolanderi* is a plant of the immediate region of the sea coast; where this species leaves off in the north, *L. ochropetalus* appears to begin. *L. sulphureus*, however, although found in the Humid Transition is more common in the Arid Transition, particularly so in California, and sometimes extends into the Upper Sonoran, as at Auburn, California. As has been mentioned, the calyx teeth of *L. Bolanderi* and *L. ochropetalus* are very similar in shape and size, but *L. sulphureus* has very different calyx teeth; they are shorter and not so broad. There are forms of *L. sulphureus*, however, which, although having the small flowers which are so characteristic, yet have calyx teeth strongly suggesting those of *L. Bolanderi*. These forms may be hybrids, but at any rate show that these species are closely allied. *L. ochropetalus holochlorus* seems to be only a form of *L. sulphureus* with very thin leaflets. The specimen cited by PIPER does have thin leaflets, but another specimen collected in 1918 by LAWRENCE from a similar locality has the coriaceous leaflets of *L sulphureus*.

The following material of *L. ochropetalus* has been examined:

WASHINGTON.—King County: Seattle, 1891, *Piper* 482 (US 218905 and 202210); same locality, June 1892, *Mosier* (US).

OREGON.—Coos County: Myrtle Point, June 1893, *Holzinger* (US); Curry County: Gold Beach, *Hoyt* (RVB); Jackson County: Antelope Creek, June 1898, *Applegate* 2361 (US).

22. LATHYRUS SULPHUREUS Brewer; A. Gray, Proc. Amer. Acad. **7**:399. 1867.—*L. ochroleucus* var. Torr., Pac. R. R. Rep. **4**:77. 1857; *L. ochroleucus* of various authors, not Hooker; *L. ochropetalus holochlorus* Piper, Proc. Biol. Soc. Wash. **31**:190. 1918.—Perennial, nearly glabrous and somewhat glaucous; stems slender, climbing, about a meter long; stipules half as large as adjacent leaflets, coriaceous, semi-sagittate, entire or dentate; leaflets 8 or more, ovate-lanceolate to ovate, acute, coriaceous, light green on both surfaces; tendrils well developed, usually branching; peduncles shorter than or as long as leaves, bearing 7–19 yellowish flowers; flowers 10–12 mm. long; calyx teeth unequal, upper 2 very short, triangular, lateral linear-lanceolate, scarcely as long as tube, ventral tooth narrowly linear, as long as or longer than tube; pods 6 cm. long, glabrous; seeds 6–7.—Figs. 23, 25.

Western Washington and Oregon to southern California; Humid Transition, Arid Transition, and Upper Sonoran Zones. April–July. Type locality, "In woods along foothills of Sierra Nevada."

For many years *L. sulphureus* has been confused with *L. ochroleucus*, which is quite different. *L. ochroleucus* may grow in this region, and the one specimen I have listed of *L. sulphureus* from Washington is very close to it. The only specimens of the true *L. ochroleucus* that I have observed in the field were in Wisconsin. The leaflets of *L. ochroleucus* are thin and obtuse, usually very broad, and are nearly always in three pairs.

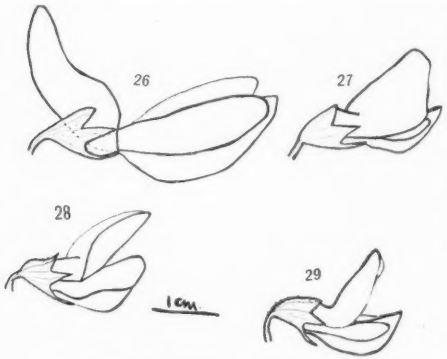
WASHINGTON.—Okanogan County: Loomis, June 1902, *Griffiths* and *Cotton* 337 (US).

OREGON.—Benton County: Corvallis, May 1916, *Gilbert* 115 (US); same locality, May 1918, *Lawrence* 1459 (US, DS); Curry County: Brookings, May 1915, *Thompson* 206 (DS); Douglas County: Glendale, June 1896, *Howell* (DS); same locality, June 1895, *Howell* 160 (UC); Lane County: Eugene, April 1905, *Sweetser* (UO); Springfield, May 1920, *Bradshaw* 1451 (RVB); Marion County: Quinaby, April 1915, Nelson (DS); Washington County: Forest Grove, May 1883, collector not given (UO).

CALIFORNIA (a greatly abbreviated list).—Amador County: locality not given, May 1893, *Hansen* 12 (DS, CA); Butte County: Berry Canyon, near Clear Creek, May 1902, *Heller* and *Brown* 5485 (US); Calaveras County: Mokelumne Hill, *Blaisdell* (CA); Fresno County: Pine Ridge, June 1900, *Hall* and *Chandler* 287 (UC); Glenn County: locality not given, June 1915, *Heller* 11994 (DS); Kern County: Green Horn Mts., *Palmer* 47 (US, UC); Lake County: near Snow Mt., June 1891, *Brandegee* (UC); Los Angeles County: Mazana, Antelope Valley, May 1896, *Davy* 2463 (UC); Mariposa County: Benton Mills, April 1883, *Congdon* (DS); Nevada County: Comptche, June 1906, *Walker* 253 (UC); Placer County: Blue Canyon, June 1908, *Walker* 299 (UC); Plumas County: Greenville, August 1920, *Clemens* (CA); Shasta County: Kennet, May 1913, *Smith* 160 (CA); Siskiyou County: locality not given, May 1909, *Quinyly* 707 (UC); Sutter County: north side of Marysville Buttes, May 1914, *Heller* 11370a (DS); Tehama County: Red Bluff, June 1917, *Wickes* (CA); Trinity County: east Weaver Creek, May 1914, *Yates* 480 (US); Tuolumne County: near French Flat, April 1919, *Ferris* 1584 (DS); Yosemite: Eightmile, June 1911, *Hall* 8985 (UC).

23. LATHYRUS SPLENDENS Kellogg, Proc. Calif. Acad. 7:90. 1876.—*L. venosus grandiflorus* Torr. Pac. R. R. Rep. 77. 1857.—Perennial, glabrous to puberulent; stems climbing, 1–3 m. long; stipules much smaller than adjacent leaflets, lower lobes denticulate or laciniate, semi-sagittate, acute to acuminate, very veiny and coriaceous; leaflets 4–10, linear-lanceolate to ovate, firm and with prominent veins, about 2–5 cm. long; tendrils well developed; peduncles

stout, 5–20 cm. long, much exceeding leaves; flowers 5–12 in the raceme, purple or dark red, very showy, over 3 cm. long; calyx teeth unequal, upper teeth broadly triangular, lateral not quite so broad, lowest linear-lanceolate to subulate, none longer than calyx tube; pods glabrous, 9 or more cm. long by 1 cm. wide; seeds about 15.—Fig. 26.



FIGS. 26–29.—Fig. 26, *L. splendens;* fig. 27, *L. laetiflorus Alefeldi;* fig. 28, *L. laetiflorus;* fig. 29, *L. laetiflorus Alefeldi* (form with narrow leaflets).

Southern California, Lower California, and Mexico; Upper Sonoran Zone. May–July. Type locality, southern California.

L. splendens, L. laetiflorus, and what has been known as *L. Alefeldi* constitute a very distinct group of American species of *Lathyrus*. The foliage of all of them is similar, and the structure of the calyx teeth and flowers indicates a decided relationship. The shape of the flowers is very much unlike that of our other species. When *L. splendens* is in full bloom, the standard pushes back so that it rests nearly in a straight line with the wings. Although *L. splendens* is quite distinct from the other members of this group, there are specimens that appear to be somewhat intermediate. Among these can be cited Miss EASTWOOD'S no. 9433. In general appearance this suggests *L. splendens,* but the flowers are entirely too small to be included with that species. *L. Alefeldi* and *L. laetiflorus* intergrade in such a way that at times they can scarcely be told apart; hence it seems desirable to give *L. Alefeldi* but subspecific rank, since the chief difference is only a matter of color.

A vast amount of the material that has passed as *L. violaceus* from southern California is really what I should call *L. laetiflorus Alefeldi.* The latter has also been confused with *L. splendens* by many collectors. Some botanists speak of *L. laetiflorus Alefeldi* as the little flowered *L. splendens.* The distribution of these species is different, however; *L. splendens* is not found so far north.

The following specimens will give an idea of the California distribution of *L. splendens.*

Imperial County: Summit, June 1917, *McGregor* 957 (DS); San Diego County: Campo, June 1880, *Parish* 1638 (DS); Potrero, May 1893, *Alderson* (DS); Potrero Grade, June 1913, *Hall* 9410 (UC).

24. LATHYRUS LAETIFLORUS Greene, Erythea 1:105. 1893.—Perennial, glabrous or puberulent; stems stout and climbing, several

meters long, branching; stipules small, not half so large as adjacent leaflets, commonly toothed, acuminate; leaflets 5–10, oblong to ovate, obtuse or acute, very firm and coriaceous, strongly venulose, 1–5 cm. long; tendrils well developed, long and divided; peduncles rather stout, 10–20 cm. long, frequently twice length of leaves; flowers 5–12 in the raceme, white or pink, 20–25 mm. long; calyx teeth unequal, upper 2 very short, lateral and ventral as long as calyx tube or less, very variable as to shape; pods flattened, slightly pubescent; seeds 4–8.—Fig. 28.

Southern California and northern Lower California; Upper Sonoran Zone. January–July. Type locality, seeds collected in Los Angeles County were germinated, and the plants raised at the University of California.

CALIFORNIA.—Los Angeles County: Mt. Wilson, Sierra Madre trail, June 1914, *Smith* 2865 (CA); Claremont, March 1916, *Cox* (US); Pasadena, Arroyo Seco, April 1903, *Hall* 3742 (UC, UO); Lincoln Park, May 1902, *Grant* (DS); plants grown at Berkeley, from seeds collected in Los Angeles County, May 1893 (UC); Orange County: Santiago Peak, June 1901, *Abrams* 1813 (DS); Riverside County: near Riverside, 1889, *Hosp* (UC); Santa Barbara County: Santa Cruz Island, June 1918, Mrs. *Miller* (CA); San Bernardino County: San Bernardino Valley, April 1906, *Parish* 5589 (UO); San Diego County: Fall Brook, November 1891, *Parish* (UC); Ventura County: piñon belt, Mt. Pinos, June 1905, *Hall* 6428 (UC).

24a. **Lathyrus laetiflorus Alefeldi** (White), n. comb.—*Orobus californicus* Alef., Bonplandia **9**:146. 1861, excl. syn.; *L. Alefeldi* White, Bull. Torr. Bot. Club **21**:449. 1894.—This subspecies is similar to the species, save that the flowers are blue or purple, and slightly larger (2–3 cm. long), and the stipules more variable in size, frequently attaining one-half the size of the adjacent leaflets.—Figs. 27, 29.

Southern California, northern Lower California, and Santa Catalina Island; Upper Sonoran Zone. March–July. Type locality, San Diego, California.

CALIFORNIA.[9]—Los Angeles County: Avalon, Santa Catalina Island, April 1901 *Grant* (DS); Gawanza foothills, June 1903, *Palmer* (UC); San Fernando Valley, February 1861, *Brewer* 199 (CA); Soledad, April 1882, *Jones* 3575 (US, CA); Riverside County: San Jacinto Mts., June 1901, *Hall* 2153 (US); San Bernardino County: San Bernardino, May 1882 (UC 15350); San Diego County: Warner's Ranch, June 1913, *Hall* 9427 (UC); San Miguel Mountain, May 1904, *Chandler* 5274 (DS); Mission Hills, May 1903, *Abrams* 3417 (DS).

PALO ALTO, CALIFORNIA

[9] Space does not permit the citation of the quantities of material of this abundant species and subspecies, or that of *L. splendens*, and the various other species which I have examined.

BRITTLE RACES OF OENOTHERA LAMARCKIANA

HUGO DE VRIES

Brittleness is a quality which belongs to the central group of characters in *Oenothera*, as distinguished by BOEDIJN and the writer (**9**). Like almost all the members of this class, it is not accompanied by the doubling of a chromosome. Moreover, it is recessive and isogamic, and therefore can be combined in the mutant races with any other mark. This article reports the study of its relations to the lethal factors, which are also situated in that group. This study starts from two races, one of which (*O. similis*) has been found in the original field at Hilversum, lately described by UPHOF (**2**), while the other (*O. scindens*) originated in my experimental garden at Amsterdam. These races are to be considered as due to recombinations of mutated qualities, the first origin or premutation of which is probably as old as the parent species itself. Secondary changes may accompany them, but they are not of paramount interest for the present study.

Oenothera Lamarckiana similis

In crosses of individuals of the same family of *O. rubrinervis* with *Lamarckiana* plants from various sources, and with different mutant strains, I observed that in the first generation sometimes brittle *rubrinervis* are produced, but in other cases tough hybrids of the type of *subrobusta* instead of *rubrinervis* (**3**). From a single cross between two individual parents both types are never seen to arise in the first generation. Moreover, the two contrasting cases have occurred mainly in strains derived from different initial plants (**3**). *Rubrinervis* is only a brittle form of *subrobusta*, and this latter usually splits off brittle specimens in the second generation. On the other hand, we have to consider *O. erythrina* (**5**), which is a mutant externally very like the hybrid *subrobusta*. It never arose by way of mutation from the main strain of *O. Lamarckiana*, which I am still using for my cultures, and which produces regularly brittle mutants of the type of *rubrinervis*. From rosettes collected at the original station near Hilversum in 1905, however, it sprung in one instance

in two specimens in 1907, and from another rosette in three individuals in the third generation in 1917. From one of the two first ones my family of *erythrina* has been derived.

Those initial rosettes of 1905 which produced *erythrina* mutants instead of brittle ones, might be considered as constituting a special mutant race, sprung in the field from the ordinary *Lamarckiana*. Of one of them seeds were no longer available, but in the third generation derived from the other in 1917, I have made some crosses, besides self-fertilizing some flowers in order to continue the race. I shall call this race *O. Lamarckiana* mut. *similis*, since it is externally an exact copy of its parent species, differing from this in no visible character and at no single period of its development. Now the question arose, whether the production of tough or brittle hybrids is connected with that of throwing off tough or brittle mutants. If this were so, we should expect the normal *Lamarckiana* to give, as it does, brittle specimens in both cases, but the production of tough mutants and tough hybrids to be a character of our new type *similis*. In order to try this it was, of course, only necessary to cross this new race with *O. rubrinervis*.

I made the cross in 1917, using my typical strain of *O. rubrinervis* as a pollen parent. Next year I had a culture of 180 plants, about one-half of which have flowered, since 111 specimens of the type of *Lamarckiana* had to be removed before the flowering period in order to save space. They constituted three main types: *Lamarckiana* and *lucida*, which were to be expected, and *subrobusta*. No brittle specimen was found. Two mutant individuals occurred, belonging to the types *albida* and *oblonga*. From this we may conclude that the new mutant strain *similis*, which produces *erythrina* instead of *rubrinervis* as mutants, also gives *subrobusta* instead of brittle hybrids in the corresponding crosses.

The seeds of *O. similis* contain the same amount of barren grains as those of *O. Lamarckiana*. In the harvest of the third generation of 1917, I counted 39, 39, 50, and 53 per cent, giving an average of 45 per cent; and in that of the fourth generation in 1921 I counted 60 per cent of empty seeds. This leads to the conception that *similis* has essentially the same constitution as its parent, and consists of *laeta* and *velutina* gametes, but without the factor for brittleness.

We should therefore expect the result of the cross to comply with the following interpretation: *similis* (=*laeta*+*velutina*)×*rubrinervis* (=*deserens*+*velutina*), giving *laeta*×*deserens* (=*lucida*)+*laeta*×*velutina* (=*Lamarckiana*)+*velutina*×*velutina* (=barren grains)+*velutina*×*deserens* (=*subrobusta*). Such was exactly the result. I counted the empty seeds, produced by the cross, on two individual plants and found 48 and 65, or an average of 56 per cent. The numerical proportions were found to be, besides the 56 per cent barren grains, 32 per cent *Lamarckiana*, 9 per cent *subrobusta*, 2 per cent *lucida*, and 1 per cent mutants. These figures differ from the expectation of four groups of equal size, but the deviations are in the same sense as in other crosses, the *velutina* (barren grains) giving, as a rule, too high, but the *lucida* too low figures (**8**).

In order to compare *O. similis* more closely with *O. Lamarckiana*, I have studied its crosses with *O. Lamarckiana* mut. *nanella*, and its mutability after self-fertilization. I failed to discover any differences. After fertilizing *O. similis* with the dwarfs of my race, I got in the first generation partly tall plants and partly dwarfs, the number of the latter being exceptionally high (90–94 per cent). In the second generation both types gave a uniform progeny. After crossing the tall hybrids with their dwarfish sisters, I found the same proportion, the offspring consisting of 94 per cent dwarfs and 6 per cent tall specimens. The types were the same as those of the crosses of my typical race of *O. Lamarckiana*.

The mutability was studied in the seeds of the second generation, cultivated as biennial plants in 1913–1914. From five specimens of *similis* I had after self-fertilization 0.7–1.1 per cent *nanella*, 0.2–0.3 per cent *lata*, 0.3–0.5 per cent *albida*, 0.5–1.0 *oblonga*, a single specimen of *semigigas*, but no *rubrinervis*. The seeds of four self-fertilized plants of 1917 gave, among 936 seedlings, 0.5 per cent *nanella*, 0.9 per cent *lata*, 0.1 per cent *albida*, 1.1 per cent *oblonga*, 1.3 per cent *scintillans*, and no *rubrinervis*. It is evident that, apart from the brittleness, the mutability of *O. similis* is the same as that of *O. Lamarckiana*. We may therefore safely conclude that *O. Lamarckiana* mut. *similis* corresponds in almost all respects with its parent species, differing only in the factor for brittleness. This latter is present in *Lamarckiana* but absent in *similis*. For this reason

O. similis may be considered to be an atavistic mutant. The ancestors of *O. Lamarckiana* must have acquired the factor for brittleness at some period; their descendants might lose it at any time.

Returning to our formula, the difference between the two types must be looked for in the *velutina* gametes, since the *velutina* × *deserens* give *subrobusta* in the crosses of *O. similis*, whereas the corresponding combination gives *rubrinervis* in the crosses of pure *Lamarckiana*. The three remaining combinations are the same in both cases. In other words, *O. similis* is a mutant which lacks in its *velutina* gametes the factor for brittleness which is so characteristic of *O. Lamarckiana*.

Oenothera Lamarckiana scindens

This is a race which is externally like a pure *Lamarckiana*, but produces only a very small amount of barren seeds. It originated from a cross made in 1913 between my pure races of *Lamarckiana* and *rubrinervis*. The seeds were sown in 1916, and yielded 32 per cent *Lamarckiana*, 20 per cent *lucida*, and 48 per cent *rubrinervis*. In this respect there was no deviation from the ordinary rule. Of the *Lamarckiana* type, only three specimens were self-fertilized. Two of them produced 66 and 75 per cent of empty seeds, as might be expected. The third, however, had only 7 per cent of such seedlike structures. From this it was evident that a new type had arisen, and a pure strain had since been derived from it. It is to this strain that later the name of *scindens* was given.

According to RENNER (1), the barren seeds of our plants contain small fertilized germs. The failure of their development is due to lethal factors, of which there are two in *O. Lamarckiana*. One of them is linked with the factors for narrow leaves and other characteristics shown in the hybrids of the type *velutina*, and the second one with the broad foliage and other peculiarities of the hybrids of the stature of *laeta*. In *O. Lamarckiana* the amphi-*velutina* and the amphi-*laeta* germs are killed by their respective lethals, and only the combination of the two components produces viable seeds. From these considerations it is evident that the new *scindens* must lack one of the lethals of its parent. Furthermore, the germs of *velutina* are usually produced in too large proportions, but those of

laeta in too small numbers, as compared with the figures for ordinary monohybrid splitting (**8**). Thus the fact that only 7 per cent of barren grains were counted, indicates that the seeds with germs of *velutina* had become viable, while those with *laeta* germs had not suffered any change in their lethal factor. In other words, *O. scindens* is distinguished from *O. Lamarckiana* by the lack of the lethal factor of the *velutina* gametes. It is probable, of course, that this change was accompanied by one or more minor mutations, but these must be left out of consideration in our present discussion. The race must thus split off viable seedlings of *velutina*, besides a small amount of *laeta* germs in the barren grains. The description of its pedigree will prove the exactness of this conclusion. I propose to

TABLE I

PEDIGREE OF OENOTHERA LAMARCKIANA MUT. SCINDENS IN PERCENTAGES

GENERATION	YEAR	SIZE	BARREN SEEDS	SCINDENS	TARDA	MUTANTS
.....	1913	rubrinervis×Lamarckiana	.....	.....	.....	.....
1.....	1916	1 mutant	.....	.....	.....	.....
2.....	1917	160 Ex.	7	50	35	8
3.....	1918	120 Ex.	5	40	48	7
3.....	1920	121 Ex.	2	43	52	3
4.....	1921	40	2	.....	.....	.....
5.....	1924	60	10	51	39	.....
Averages	.....	.....	5	46	43	6

give the name of *O. Lamarckiana* mut. *tarda* to the split off *velutina*, which constitutes a new strain.

I shall first give the pedigree in its most condensed form, indicating the percentages as calculated for the whole harvest, and giving the size of each culture. In 1917 and 1918 almost all of these plants flowered and ripened their fruits, but in repeating the third generation in 1920, only a smaller number were planted out. Every new generation was sown from seeds of a specimen of the type *scindens*, self-fertilized in the previous one. The third generation has been cultivated twice, in 1918 and 1920. The amount of barren grains was determined in glass tubes at about 30° C., containing 100 seeds each.

The mutants in the second generation were *lata*, *nanella*, *oblonga*, *pallescens*, and *lucida*-like, but in 1918 *nanella*, *oblonga*, and *lucida*-

like, and in 1920 *lata*, *lucida*-like, and *oblonga*. The *lucida*-like plants had almost no sterile seeds (0–5 per cent) after self-fertilization; they indicate the copulation of gametes, mutated into a brittle form. It is evident that the mutability of *O. scindens* is at least as efficient as that of the parent species. The loss of the lethal factor for *velutina* has not changed this quality.

In 1917 I fertilized 28 specimens of the type of *Lamarckiana* with their own pollen, and counted the barren seeds for each of them. Their number varied from 0 to 8 in 100 seeds, giving an average of 5 per cent, determined in a total of 2800 seeds. I also counted the seedlings in the types of *Lamarckiana* and *tarda* for each of the 28 samples separately, and found 33–53 per cent of the first and 47–67 per cent of the second form, with an average of 42 per cent *scindens* and 58 per cent *tarda*, as determined from about 3000 seedlings. By the introduction of the barren grains and the mutants into the calculation, these figures become changed into those given in table I. It is evident, however, that they indicate equal groups of the two main types. The same conclusion follows from the average of the harvest of the different generations.

Both *scindens* and *tarda* constituted uniform types, which remained the same during all the generations. No external characteristics were discovered on which a distinction of *scindens* from *Lamarckiana* could be founded. If we try to express the result of our cultures in a simple formula, giving the constitution of *O. scindens*, and call the mutated *velutina* gametes *tarda*, we get the formula: *O. scindens* = *laeta* + *tarda*. In this formula our race is assumed to be isogamic like its parent. After self-fertilization it must then split into 50 per cent *laeta* × *tarda* = *scindens*, 25 per cent *tarda* × *tarda*, and 25 per cent *laeta* × *laeta*, which last constitute the barren grains. The deviations of our figures from this calculation may be explained by the fact that *laeta* germs are produced ordinarily in too small numbers, whereas the proportion of *velutina* is often far above the expectation (**8**).

In order to control the exactness of these conclusions, I have made a series of crosses, partly with other species, and partly with *O. Lamarckiana* and some of its mutants. The first group produced hybrids of the types of *laeta* and *velutina*, respectively *densa* and

laxa, which were exactly the same as the corresponding hybrids of the parent species, cultivated beside them for comparison. The results are combined into tables II and III. In the case of *O. scindens*×*O. Hookeri*, the seedlings of crosses on four different individuals were separately counted. There were no essential differences, and only the average figures are given. In the cases of *O. scindens*×*O. biennis Chicago*, some of the *laeta* and some of the *velutina* were self-fertilized

TABLE II

CROSSES OF O. SCINDENS WITH OTHER SPECIES

O. SCINDENS×	CROSS	PERCENTAGE OF		SIZE OF CULTURE
		laeta	velutina	
O. biennis Chicago	1920	13	87	60 Ex.
O. Cockerelli	1920	33	67	60 Ex.
O. Hookeri	1917	38	62	237 Ex.
Average	.....	28	72	.....

TABLE III

CROSSES OF OTHER SPECIES WITH O. SCINDENS

×O. SCINDENS	YEAR	PERCENTAGE OF	
		laeta	velutina
O. biennis	1917	49	51
O. syrticola	1917	45	55
O. biennis Chicago	1920	58	42
O. Cockerelli	1917	58	42
O. Cockerelli	1920	43	57
O. Hookeri	1917	20	80
O. Hookeri	1920	27	73
Average	.....	43	57

in 1921; their seeds contained 8 per cent and 2 per cent of sterile grains respectively.

In all these experiments the culture of the hybrids embraced 59–60 seedlings. Those of *O. biennis Chicago*×*scindens* had the types of *densa* and *laxa*. Comparative cultures of the corresponding hybrids of *O. Lamarckiana* were used for the identification. I self-fertilized some specimens in the cultures of 1920, and found only a small amount of barren grains for both types in each of them. From these figures it follows that *O. scindens* has about an equal amount of

gametes of the types of *laeta* and *velutina* among its pollen, but the reciprocal crosses show a deviation from the expectation corresponding to the preferential fertilization in the *velutina* gametes (8).

We may now consider the crosses with *O. Lamarckiana* and some of its mutants. In the first place, I have chosen *O. blandina*, which is a homogeneous race, and three other mutants, in which the active pollen is also homogeneous. I shall first give the numerical results, and afterwards compare them with the expectation as derived from our formula.

The crosses were made in 1920 and 1921, and 60 specimens of each of the cultures have flowered. The first two cases are explained by the formula (*laeta*+*tarda*)×*blandina*, giving *laeta*×*blandina* or

TABLE IV

HOMOGENEOUS CROSSES OF OENOTHERA SCINDENS

CROSSES	PERCENTAGE OF		BARREN GRAINS
	Lamarckiana-like	blandina and tarda	
blandina×scindens	35	65 (blandina)	.....
scindens×blandina	12	88 (blandina)	.....
scindens×candicans	13	87 (tarda)	2
scindens×secunda	100	0	11
scindens×elongata	100	0	8

laeta rediviva, which is almost like *Lamarckiana*, and *tarda*× *blandina*, which must be expected to be like *velutina*×*blandina*, having the stature of the latter form, and showing an excess of individuals, according to the general rule for both *blandina* and *velutina*.

The cross *scindens*×*candicans* was made in order to prove directly the absence of one of the lethal factors in the *tarda* gametes. *O. candicans*, the formula for which is *O.* (*candicans*+*velutina*)× *velutina* (7), has only pollen of the type of *velutina*, containing the normal lethal of these gametes. If *tarda* possessed the same lethal their combination would yield barren grains, but no viable plants of either type. Barren grains were almost absent, and 87 per cent of the type of *tarda* were produced. This percentage shows the same deviation from expectation as in the two previous crosses, but the main result is that *tarda*×*velutina* gives viable plants, proving that

the lethal of the latter is absent in the former. The other type of the hybrids was *laeta*×*velutina*, giving ordinary *Lamarckiana*.

Secunda and *elongata* are derivatives from *O. simplex* (6). The viable part of their pollen consists of *laeta* gametes only. Combined with *O. scindens*, it must produce *laeta*×*laeta* or barren grains and *tarda*×*laeta* or *scindens*. The barren grains were to be expected in the same percentage as in *O. simplex* itself after self-fertilization, and such was exactly the case. The cultures on the beds were uniformly *scindens*, which, as has been stated, cannot be distinguished in the garden from *O. Lamarckiana*.

A most interesting cross is that with *O. deserens* (4), which is a uniform race, with only one kind of gametes. These contain the factor for brittleness, but have no lethal. Combined with *velutina*

TABLE V

CROSSES OF O. SCINDENS WITH O. DESERENS

CROSSES	PERCENTAGE OF	
	lucida	brittle
O. scindens×deserens	15	85
O. deserens×scindens	45	55

they produce *O. rubrinervis*, from which the strain has originally been split off. The combination with *scindens* must therefore be expected to yield *laeta*×*deserens*, a common hybrid which I have more than once described under the name of *lucida* (4), and *tarda*×*deserens*. This latter combination has the factor for brittleness, which is recessive, on both sides, and must therefore produce brittle plants, which must be expected to comply in their main feature with the type of *O. velutina*×*deserens*=*O. rubrinervis*. Both the expected types of hybrids occurred, as was evident from a comparison with the corresponding hybrids of *O. Lamarckiana*×*O. rubrinervis*.

The crosses were made in 1920, and from each of them I had in the following summer a lot of 60 flowering hybrids. The brittle specimens are in excess, as was to be expected.

With *O. Lamarckiana*, *O. nanella*, and *O. lata*, the results, of course, are of a more complicated nature. I made the combinations shown in table VI in the summer of 1917.

The crosses with *O. nanella* were made with pollen of two differ-

ent strains. The hybrids were counted in the period of well developed rosettes, in which the distinguishing features were bright and clear. The barren grains are given in percentages of the whole harvest. The first two crosses must be expected to give the same results, since both parents are isogamous. The expectation would be for equal groups of *laeta*×*laeta* = barren grains, *laeta*×*velutina* = *Lamarckiana*, *tarda*×*laeta* = *scindens*, and *tarda*×*velutina* = *tarda*. The types of *Lamarckiana* and *scindens* are exactly the same, and cannot be separated on the beds; the *tarda* appear in too large numbers, as usual.

In the crosses between *Lamarckiana* and *nanella*, a certain number of dwarfs are usually produced in the first generation, and

TABLE VI

CROSSES OF O. SCINDENS WITH O. LAMARCKIANA, O. NANELLA, AND O. LATA

CROSSES	PERCENTAGES OF		TARDA	BARREN GRAINS	SIZE OF CULTURE
	Lamarck-iana	nanella, lata			
O. scindens×Lamarckiana..	38	0	62	1–11	100 Ex.
O. Lamarckiana×scindens..	50	0	50	4–7	100 Ex.
O. scindens×nanella.....	11	13 (nanella)	76	8	71 Ex.
O. scindens×nanella.....	22	20 (nanella)	58	2	71 Ex.
O. lata×scindens.....	43	35 (lata)	22	14, 17, 34	106 Ex.

therefore might be expected here also. If we combine them with the figures for *Lamarckiana*, the results are essentially the same as in the two previous crosses.

The cross with *lata* may be compared with the crosses of this mutant with other species, which yield three types of hybrids (3): *laeta*, *velutina*, and *lata* in almost equal numbers (6). From this the expectation for our cross would be: (*laeta*+*velutina*+*lata*)× (*laeta*+*tarda*) = *laeta*×*laeta* (empty seeds), *laeta*×*tarda* (= *scindens*), *velutina*×*laeta* (or *Lamarckiana*), *velutina*× *tarda* (= *tarda*), *lata*× *laeta*, and *lata*×*tarda*. The last two must reproduce specimens of the type of *lata*. If we calculate these figures on the whole harvest, we get in percentages:

Counted: 21 barren grains; 36 *Lamarckiana*+*scindens;* 16 *tarda;* 27 *lata*
Expected: 17 barren grains; 33 *Lamarckiana*+*scindens;* 17 *tarda;* 33 *lata*

The conformity of the two groups of figures is quite evident.

Considering the results of all our crosses, we find that they give proof of the isogamic condition of our new race *scindens*, and comply with its formula *laeta*+*tarda*. In this the *laeta* gametes do not show any difference from those of *O. Lamarckiana*, but the *tarda* gametes differ from *velutina* in the absence of the lethal factor.

Splitting in O. Lamarckiana tarda

About one-third of the seedlings of *O. scindens*, reported in table I for 1917, had the low stature and brittle stems characteristic of *O. tarda*. From one of them I have derived a self-fertilized strain, which I cultivated during three further generations and used for some crosses, in order to study its constitution. In these cultures the *tarda* have split off a new form of the same stature and brittleness, but lacking the reddish tinge on the younger parts, and especially on the flower buds, and with broader foliage. I have called this form *pallida*. Table VII records the results of the repeated self-fertilizations in the race of *tarda*.

TABLE VII

PEDIGREE OF O. LAMARCKIANA SCINDENS MUT. TARDA

GENERATION	YEAR	SIZE OF CULTURE	SEED-BEARERS	PERCENTAGE OF PALLIDA
1	1917	Mutants	2	.....
2	1922	115	2	23
3	1923	60	10	42
4	1924	600	.....	27

The percentages are averages from the separate countings of the progeny of the seed-bearers of the previous year. In the third generation I fertilized ten specimens, in order to know whether some of them might have a uniform offspring. This was not the case. The amount of *pallida* differed between 20 and 30 per cent, with an average of 27 per cent.

From table VII we may deduce that the *pallida* is split off after the formula: *tarda* = (*tarda* + *pallida*), which should give, after self-fertilization, 25 per cent of pure *tarda*, 50 per cent of *tarda* × *pallida*, and 25 per cent of pure *pallida*. The first combination must result in barren grains, since no living specimens of it were observed. The

empty seeds amounted to 2–5 per cent in the harvest of 1917, 1–9 per cent for eight of the ten plants of 1923, and 14 and 24 per cent for the two others. On the average the percentage was 8. From this we conclude (8) that the lethal factor was that of the *laeta*, the same as in the parent *scindens* and the grandparent *Lamarckiana*, but which fails in most of the original mutated gametes of *scindens*.

The offspring of the type *tarda* × *pallida* continued the race, while the *pallida* must be uniform and constant, having only recessive characters. In 1922 I fertilized two specimens of it, and had in the two following years the second and third generations, with 60 and 44 flowering plants, all of which were true to type. From this it is clear that no lethal factors could occur in *pallida*. Besides this, some other mutant strains without lethals are known. They are often used in crosses. They are combined in table VIII.

TABLE VIII

HOMOGENEOUS STRAINS DERIVED FROM O. LAMARCKIANA

A: LAETA	B: VELUTINA
1. *decipiens*, tough	3. *blandina*, tough
2. *deserens*, brittle	4. *pallida*, brittle

The group is thus seen to be completed by our new strain.

In 1922 I made some crosses with *O. tarda* of the second generation, in which I combined it with *O. blandina* and with different species, and had in 1923 a culture of 60 flowering plants for each of them. All of these 480 plants showed the stature and characters of the *velutina* from the corresponding crosses of *Lamarckiana*, which were cultivated on a separate bed near to them, in order to compare them in every phase of their development. No *laeta* plants were found. Only a part of the *velutina*, however, were exactly like their type, since another part had a broader foliage, the leaves reaching about half the breadth of the corresponding *laeta*. Table IX gives the results of the countings.

No brittle plants were found, since this character is recessive. In the first cross the hybrids had the type of *laxa*, as was to be expected. From table IX it is evident that *tarda* is isogamic, the reciprocal crosses giving the same result, and has two kinds of gametes in about equal numbers, corroborating the formula given. The difference between these two kinds of gametes, however, is

much smaller than that between the gametes of either *scindens* or *Lamarckiana*, almost all of their characters belonging to the category of *velutina*. This is corroborated by the results of other crosses. *O. tarda*×*elongata* gave an almost uniform progeny of the type of *Lamarckiana*. *Elongata* is a *laeta* type, with uniform pollen, and must give with the *pallida* the combination *velutina*×*laeta*, since the brittleness is recessive. There were 6 per cent of barren seeds and some mutants.

O. tarda×*tardescens* produced a dimorphic progeny with some mutants, which, however, did not flower. Among the 51 flowering individuals, 39 showed the marks of *tarda* and 12 those of *pallida*.

TABLE IX

CROSSES OF O. TARDA WITH OTHER SPECIES

CROSSES	VELUTINA	BROAD LEAVED
O. biennis Chicago×tarda	27	33
O. Cockerelli×tarda	26	34
O. Hookeri×tarda	33	27
O. muricata×tarda	24	36
O. blandina×tarda	31	29
tarda×O. biennis Chicago	34	26
tarda×O. Hookeri	30	30
tarda×O. blandina	27	33
Totals	232	248
Percentage	49	51

O. tardescens has only *velutina* gametes in its pollen, and their special marks were evidently recessive to those of the components of *O. tarda*.

O. tarda×*deserens* and its reciprocal also reproduced the two types of *O. tarda*, among 53 and 60 flowering specimens giving 50–60 per cent *tarda* and 40–50 per cent *pallida*. *O. deserens* has the same stature and brittleness as *O. tarda*, but no lethal.

O. tarda×*O. Lamarckiana* and its reciprocal cross yielded plants of the types of both parents, in cultures of 54 and 52 flowering plants giving 40–60 per cent *tarda* and 60–40 per cent of the *Lamarckiana* type. The calculation for this cross is *tarda*×*laeta*, *tarda*×*velutina*, *pallida*×*laeta*, and *pallida*×*velutina*. The first combination must give barren grains, the second must give the type of

tarda, the third that of *Lamarckiana*, and the fourth combination evidently results in specimens of the type of *tarda*, since no plants like *pallida* were found. Thus we see that the different crosses prove the formula for *O. tarda* = *tarda* × *pallida*, as already given.

Conclusion

The genetical constitution of the three races may be expressed as follows: *scindens* = *laeta* + *tarda*; *tarda* = *tarda* + *pallida*; and *pallida* = *pallida*.

The factors involved in the origin of these races are (1) for *laeta* the same as in *O. Lamarckiana;* (2) for *tarda* the same as in the *velutina* gametes of *O. Lamarckiana*, with the factor for brittleness, but with the lethal factor of the *laeta* and without the lethal factor of the *velutina;* (3) for *pallida* the same as in *tarda*, but without lethal factors, and with a factor for broader foliage and one for paleness (small amount of red color). The two latter factors may have been derived from the *laeta* gametes.

Pallida is a homogeneous race, like *deserens*, *blandina*, and *decipiens*. Of these, *deserens* is also brittle, but in *blandina* and in *decipiens* this character is absent.

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INHERITANCE OF DEFORMED LEAVES IN PHARBITIS NIL

YOSHITAKA IMAI

(WITH ONE FIGURE)

Pharbitis Nil, the Japanese morning glory, exhibits several types of variegation. Usually the variegated leaves are more or less deformed by the insertion of white tissues which develop poorly. Another deformed leaf, called "deficient," is a peculiar type of irregularity. The affected leaves are so deformed that they might be mistaken for leaves affected either by disease or an attack of insects. The abnormality, however, is transmitted quite in a Mendelian ratio. The writer will attempt later to discuss the genetic behavior of the variegated and the deficient leaves.

Two types of variegation

COMMON VARIEGATION

The recessive nature of the variegated leaf (fig. 1 *A*, *B*) to the wholly colored condition has been successively proved by several writers, including TAKEZAKI (4), HAGIWARA (1), IMAI (2), and MIYAKE and IMAI (3). In raising an F_2 from the self-colored F_1, the alternative characters were segregated in the usual ratio of 3:1. Table I gives the total data obtained in the writer's breeding experiments during the past ten years.

The raising of the F_3 generation did not give any novel results beyond expectation. The F_3 data of two crosses are summarized in table II. This table gives quite the expected results of monohybrid inheritance.

"GEJIGEJI" VARIEGATION

In several crosses of the variegated and the wholly colored leaves, however, unexpected results were obtained. The parents of these specimens of the crossing having no unusual feature, I naturally expected to obtain therefrom the simplest segregation of 3:1 in the F_2 generation. Actually, however, the results were contrary to ex-

pectation, giving the addition of a new type of variegation among the variegated segregates. As the novelty assumes fine markings of variegation, it can be differentiated clearly from the common type.

FIG. 1.—*A*, *B*, ordinarily variegated leaves, but much deformed; *C*, *D*, deficient leaves; *C*, variegated, *D*, self-colored.

TABLE I

Cross	Self-colored	Variegated	Total
RA×21–2	62	17	79
RA×M1	80	20	100
RA×IH	90	16	106
β×318	148	56	204
A×71–2	102	37	139
β×73	140	31	171
RA×71–2	219	70	289
SG×RA	53	22	75
319×170	127	43	170
α×65	81	27	108
170×A2	244	73	317
170×77	50	13	63
M2×58–2	99	30	129
M2×M4	105	37	142
S3×S5	50	13	63
65×505	302	84	386
WS×AG	37	10	47
HT×229–1	89	20	109
N113×HT	44	22	66
A4×86–2	73	20	93
65×A2	124	45	169
22–2×A2	28	12	40
22–1×A2	124	42	166
106×A2	57	21	78
22–1×A5	56	20	76
11–1×A4	105	18	123
318×13–3	85	32	117
FZ×A2	133	29	162
NT×A2	196	59	255
M3×A2	14	6	20
A1×A2	106	28	134
50×A2	279	94	373
A4×A2	151	40	191
324×316	245	69	314
319×321B	189	61	250
326×A5	490	149	639
Total	4605.00	1398.00	6003
Expected	4502.25	1500.75	6003

TABLE II

Cross	Character of F_3	Total of pedigrees	Self-colored	Variegated	Total
65×505	Self-colored	9	902	.....	902
		35	2150	656	1806
	Variegated	14	.....	780	780
324×316	Self-colored	20	646	.....	646
		40	900	297	1197
	Variegated	9	.....	89	89

This peculiar pattern of variegation reminds one of a Japanese saying "the marks left by the creeping Gejigeji" (a kind of myriapod). We might therefore call this type of variegation "Gejigeji." The observed number of such F_2 specimens was composed of three forms, the wholly colored, the commonly variegated, and the "Gejigeji" leaves, which appeared practically in the proportion of 12:3:1, a

TABLE III

Cross	Self-colored	Ordinarily variegated	"Gejigeji" variegated	Total
314×A2 1	65	18	4	87
2	27	2	2	31
3	52	22	3	77
4	63	17	10	90
RA×314	37	2	2	41
314×T5	24	6	3	33
Total	268.00	67.00	24.00	359
Expected	269.25	67.31	22.44	359

x^2=0.11; P=practically 1.

TABLE IV

F_2 DATA OF CROSS 314×A2

Character of F_2	Pedigree number	Self-colored	Ordinarily variegated	"Gejigeji" variegated	Total
Self-colored	A	18	5	.....	23
	B	8	3	1	12
	C	30	7	1	38
Ordinarily variegated	D	.....	8	.....	8
	E	.....	15	4	19
	F	.....	20	8	28
"Gejigeji" variegated	G	.....	.....	5	5
	H	.....	.....	6	6

modified dihybrid ratio (table III). To explain this result factorially the following two allelomorphic pairs may be assumed: (1) V, v.—v is a factor for the variegation, while its large letter is responsible for the wholly colored condition; (2) V_g, v_g.—This allelomorphic pair is connected with the "Gejigeji" marking; the v_g factor produces its effect on the vv-carrying plants, while on the wholly colored leaves it has no visible effects.

On the assumption that these factors are present, the genetic composition of the F_1 plants may be considered to be VvV_gv_g. Then we should expect the following combinations of the factors in the F_2:

$$(VV_g+Vv_g+vV_g+vv_g)^2=$$
$$\underbrace{1VVV_gV_g+2VvV_gV_g+2VVV_gv_g+4VvV_gv_g}_{9\text{ self-colored}}+\underbrace{1vvV_gV_g+2vvV_gv_g}_{3\text{ commonly variegated}}+\underbrace{1vvv_gv_g}_{1\text{ ``Gejigeji''}}$$

The segregating ratio of the actual numbers corresponds rather closely to the theoretical expectation. The F_3 specimens were raised in considerable numbers, but the majority of them were damaged by wandering dogs, which destroyed the seedlings by digging in the field and disturbing the labels. Only a part of them, therefore, which may assist the formulation of the above hypothesis, are given in table IV.

The F_3 data thus corresponded quite closely with the expectation. The Gejigeji variegation, due to the combined representation of two recessive factors, was thus fixed at its first appearance. In the F_2 segregation of the hybrids of the variegated and the wholly colored leaves, there was commonly the simplest ratio, as was stated in the former section, while in a few cases there appeared the Gejigeji form of variegation in addition to the two parental types. Why should we obtain such different results in apparently the same sort of matings? In considering this problem, it must be remembered that the exceptional crosses were performed invariably by utilizing 314, a pure green leafed specimen, as one of the parents. It was assumed that the factor v_g has no influence on the wholly colored leaf, and its presence cannot be detected by phenotypically examining the self-colored, VV-carrying leaves. The pedigree 314 bears the wholly colored leaf, but genetically it carries the v_g factor in the full condition; namely, the genetic composition is VVv_gv_g. On crossing this strain with the common variegated one (vvV_gV_g), we ought to obtain the self-colored leaves carrying the VvV_gv_g factors as the F_1 hybrid, and they actually do result in an F_2 consisting of three forms in the 12:3:1 ratio.

Deficient leaf

Appearance

From a packet of seeds furnished by a seedsman several plants were raised having cordate leaves. On self-fertilization they produced families which bred true to the cordate leaf. Examining the seedlings in the bed, the writer was struck with the unexpected occurrence of a few deformed cotyledons, each forming a certain peculiar shape with fine white splashes on the margin of the affected parts. Encouraged by this discovery, I transplanted all of the seedlings of the abnormal family, and watched their behavior throughout the season. This deformity occurred more frequently on the leaves, but in general its appearance was confined to only a part of the leaves of each individual. On account of the deformed condition of the leaves, this abnormality is called "deficient."[1] This deficient leaf suggests a disease appearance (fig. 1 *C*, *D*). The types of the deficient leaf are not confined to any particular shape, but it is possible for any part to be missing. As the deficiency does not appear in all leaves on one individual, however, observation must be made of every leaf throughout the plant growth, from the cotyledons to the upper leaves. The result of such an aberrant family is shown in table V. The deficient leaves thus appeared in only 10.6 per cent, where 25 per cent would be expected in the Mendelian inheritance. The deviation exceeds three times the standard error; so some statement would seem to be needed to account for the source of such an abnormal segregation.

Experimental data

One of the deficient leaves thus obtained, no. E225, was crossed with a normal leaf (M10). The F_1 plants of this reciprocal mating were quite normal, showing no deformed feature. In the following generation there occurred again some deficient leaves. The actual segregation is given in table VI.

The proportion of the deficient leaves is 12.3 per cent, the value being not more than half of that expected. The deviation again exceeds three times the standard error. Such repeated deviations

[1] The deficient leaf is not a novelty in the Japanese morning glory; this type has figured at times in literature, even in our classical books such as *Asagao Fu* (1830).

cannot be attributed to the result of mere chance sampling. For the sake of convenience of statement, the discussion on this subject will be postponed to later pages. Here let us consider the F_3 data. The raising of this generation was made from 62 F_2 plants, out of which 56 were normal and the remaining 6 were deficient. The results of these families are given in table VII. When the families including less than 10 individuals are omitted from calculation, the homozygotic and the heterozygotic normals are 13 and 20 respectively, where we should theoretically expect 11 and 22; while 4 normals (nos. 19, 25, 26, and 40), which were previously excluded from this calculation, gave entirely unexpected results. They were apparently quite

TABLE V

	NORMAL	DEFICIENT	TOTAL
Observed.....	93 (89.4 per cent)	11 (10.6 per cent)	104
Expected.....	78	26	104

$D = \pm 15.00$; $SE = \pm 4.42$.

TABLE VI

	NORMAL	DEFICIENT	TOTAL
Observed.....	138 (87.7 per cent)	18 (12.3 per cent)	146
Expected.....	109.5	36.5	146

$D = \pm 18.5$; $SE = \pm 5.23$.

normal, yet the greater part of their offspring were composed of deficient leaves, the proportion of the abnormal individuals being 87.6 per cent. Such aberrant results are quite similar to those observed in the progeny of the deficient leaves. Six deficient leaves were taken for raising the F_3 generation, and the resultant offspring contained a few normals among the deficient leaves. With reference to each deficient family, some of them bred true to the abnormality, while the others produced some normal rogues. On the average, the abnormal plants appeared in 86.15 per cent of the cases, the other 13.85 per cent being normal.

OCCURRENCE OF FALSE NORMALS

The abnormal features in the experimental data will be arranged according to four points: (1) the extracted deficient leaves of the

TABLE VII

F_3 DATA OF CROSS M10×E225

CHARACTER OF F_3	TOTAL OF PEDIGREES	NORMAL	DEFICIENT	TOTAL
	22	511	.....	511
Normal	1.....	15	4	19
	2.....	76	14	90
	3.....	43	5	48
	4.....	30	5	35
	5.....	16	10	26
	6.....	31	11	42
	11.....	2	1	3
	17.....	37	11	48
	18.....	44	7	51
	20.....	5	1	6
	21.....	4	1	5
	22.....	9	3	12
	23.....	10	4	14
	27.....	15	10	25
	29.....	4	2	6
	31.....	18	6	24
	32.....	28	6	34
	38.....	17	6	23
	41.....	8	1	9
	42.....	26	5	31
	45.....	9	2	11
	46.....	33	5	38
	47.....	52	7	59
	51.....	18	5	23
	52.....	33	6	39
	53.....	22	4	26
	54.....	3	1	4
	55.....	43	3	46
	57.....	20	2	22
	60.....	3	1	4
	Total.....	674.00	149.00	823
	Expected...	617.75	205.25	823
False normal	19.....	7	13	20
	25.....	4	28	32
	26.....	3	48	51
	40.....	2	24	26
	Total.....	16	113	129
	Expected...	0	129	129
Deficient	10.....	0	15	15
	30.....	2	6	8
	34.....	7	36	43
	39.....	0	1	1
	50.....	0	2	2
	59.....	9	52	61
	Total.....	18	112	130
	Expected...	0	130	130

segregating families were fewer than expected; (2) a few plants, which were noted as normal, gave progenies which included deficient leaves for the large part; (3) the deficient leaves sometimes did not breed true to the abnormality, producing a few individuals which appeared quite normal; (4) the results of (2) and (3) are fundamentally the same, although the phenotype of the parental plants was not common, the one being normal, while the other was deficient.

The following statements attempt to explain these unusual results. As already stated, the deficient feature is not displayed on all leaves of the individual plant; its occurrence is confined to a few leaves only. In such an abnormal state we might expect the occurrence of the exceptional plants which failed to manifest the deficient feature on the leaves throughout their plant growth. As the Japanese morning glory is an annual, dying in the autumn, its life duration is specially limited. If the species were a perennial and made practically unlimited growth, such a false normal might not be obtained. As the so-called false normals are the result of the false representation of the deficient factors throughout their development, they should produce offspring with the same characteristics as those of the deficient plants, frequently producing some false normals among the deficient descendants. In the segregating generation of the normal parents we should also expect the occurrence of false normals. This fluctuating representation should lower the value of the percentage of the deficient leaves in the segregating families.

Failing frequency

To estimate the failing frequency of the deficient representation, all available results are collected in table VIII, where the data of the progeny of the false normals are added on the assumption that they are genetically the same. Thus the estimate shows that the failing frequency on an average is 13.13 per cent.

Next we shall attempt to find the failing value from the data of the segregating normal families. When the value is represented by x, the extracted deficient leaves must be $1-x$, and consequently the normal sisters are $3+x$. From this relation we establish the following formula:

$$\frac{\text{number of normal leaves}}{\text{number of deficient leaves}} = \frac{3+x}{1-x}.$$

If we apply the F_3 result to this formula, the value of x is 0.4324, or about 43 per cent. Comparing this value with that obtained with the deficient families, the former is more than three times the latter, the difference being too great to be accounted for by mere chance sampling. Then how can we explain it? For the sake of brevity we shall call the failing proportion calculated from the data in the deficient families the "direct value," and that estimated from the results of the segregating progeny of the normals the "indirect value." This designation shows that the segregating aspect of the deficient leaves is different one from the other. In the calculation of the direct value we are dealing with the pure families for the deficient leaf, and as the operation on these was made immediately, the value may not need any qualification. The indirect value, how-

TABLE VIII

		Normal	Deficient	Total	Percentage of normal
Observed	from "false normal"	16	113	129	12.40
	from "deficient"	18	112	130	13.85
Total		34	225	259	13.13

ever, depends upon the difference of the theoretical and the observed numbers; so it might include the deviation caused by unequal mortality, or any other such cause as might be present. Strictly speaking, the so-called indirect value of failing frequency, then, might be of absolute frequency plus α. As to the reason why such a difference between the direct and the indirect values cannot be attributed to mere chance of deviation, the following statements may be added. The indirect values of the F_2 data and the segregating family of unknown origin were 70 and 57.69 per cent respectively. Comparing these frequencies with 43 per cent of the F_3 data, the respective difference is not small, and might be accounted for partly by the chance deviation due to the small number of samplings. We cannot neglect the growing condition of the plants in the different years, however, for the influence of the deficient feature may depend largely upon the plant growth. So far as the writer's data showed, the indirect value was always higher than the direct by a consider-

able percentage; this fact may be related to the actual occurrence of unequal mortality between the normal and the deficient leaves, the latter being more damaged than the former in the course of their growth. The problem as to the time when such unequal mortality was introduced (after germination or at gametic or embryonic development), and the problem as to cause (weakness in the struggle or lethal fate) must be left undecided here. If the difference between the direct and the indirect values can be regarded as the result of the influence of unequal mortality, it may represent the actual frequency of the mortality of the deficient leaves. Such a difference amounted to 30.11 per cent in the F_3 data, showing that about 30 per cent[2] of unequal mortality occurred in the deficient members of that generation. The reason why only the F_3 data are cited for the comparison is that only these were grown in the same year and produced under about the same treatment as was given to the families from which the direct value was calculated.

Summary

Under the heading of "Deformed leaves" the writer dealt with the genetic behavior of the variegated and the deficient leaves. Summing up, the results are:

1. The variegation is transmitted as a simple recessive to the wholly colored condition.

2. In some crosses of the variegated and the wholly colored leaves there appeared unexpectedly a new type of variegation, called "Gejigeji," a faint variegated pattern.

3. The Gejigeji type is caused by a recessive factor, its dominant allelomorph being a normal variegation on the common basis of the double *v*.

4. The representation of the Gejigeji pattern is limited to the variegated individuals, the effect not being apparent in the self-colored leaves.

5. The ratio in the dihybrid segregation is a 12:3:1 with reference to the wholly colored, the commonly variegated, and the Gejigeji leaves.

[2] From the fact that the homozygotic and the heterozygotic normals were obtained in the usual 1:2 ratio, this value might not be related to any gametic cause.

6. The effect of the deficient leaf factor appears in both cotyledons and leaves.

7. The deficient leaf looks just like a symptom of some disease, yet it is caused by a genetic factor. The abnormality behaves as a simple recessive to the normal.

8. The representation of the deficient feature is not manifested on all leaves of the plant, only a few leaves in one individual being affected.

9. For this reason there may sometimes be found deficient leaves which are quite normal, failing to show the proper characteristic throughout their plant growth.

10. The false normals may either breed true or produce again a few normals among the deficient offspring.

11. The failing proportion of the deficient leaves is about 13 per cent in the direct calculation, while it attains about 40–70 per cent in the indirect process.

12. The difference of two values may perhaps be mainly due to the unequal mortality of the deficient leaves. If this is the case, the so-called indirect value is of absolute frequency plus a.

13. We expect the value to fluctuate depending on the condition of the plant growth.

This investigation was made under the direction of Professor K. MIYAKE, to whom the writer wishes to express his hearty thanks. The writer is also under obligations to Mr. K. HASHIMOTO for his substantial encouragement.

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CONTINUOUS RESPIRATION STUDIES OF DORMANT SEEDS OF XANTHIUM

CONTRIBUTIONS FROM THE HULL BOTANICAL LABORATORY 340

JUNJI OTA

(WITH FOUR FIGURES)

Introduction

It has been known for some years, from the work of CROCKER (**3**) and SHULL (**6**), that the delayed germination of the upper seeds of *Xanthium* is due to certain seed coat and embryo characters connected with the supply and the need of oxygen. The low permeability of the upper seed coat to oxygen, and the high oxygen demand of the upper embryo for germination, act in conjunction in the delayed germination of these seeds. These coat and embryo characters make it possible to keep the upper seeds in germinators for months without germination taking place, unless the seed coats are broken, or the partial pressure of oxygen is increased, or some other source of oxygen supplied, as H_2O_2, or the temperature increased sufficiently to overcome the delay due to low oxygen supply.

That there may be other factors in the delayed germination is indicated by certain results reported by SHULL and DAVIS (**8**), who found that seeds which have been in the germinators for some weeks or months do not germinate as readily as fresh seeds when the coats are removed. The seeds show a tendency to dormancy of the embryos after having been in the germinator for some time without germinating. These writers followed the catalase activity of upper and lower seeds of *Xanthium* during germination and dormancy, and found that long delay of germination while in the germinators leads first to an increased catalase activity of the upper seeds, followed by a decline, which at the end of several months leaves the seeds with no more catalase activity than air dry seeds. The catalase differences between upper and lower seeds were found in harmony with the other physiological differences which cooperate to bring about delayed germination of upper seeds with intact coats. SHULL

and DAVIS suggested that the respiration rate probably followed the same course as the catalase activity, a rise soon after placing in the germinator, followed by a decline. This suggestion was no doubt based upon a preliminary study of the respiration of upper seeds by SHULL (**7**), and the fact that catalase activity very frequently parallels respiratory rates, as shown by APPLEMAN (**1**) and others. No study of the respiration of these dormant uppers over long periods in the germinator had been made, however, and indeed the respiration of dormant seeds in general has received but scant attention. Miss SHERMAN (**5**) studied the respiration of *Amaranthus retroflexus* seeds over a period of 176 days after harvesting, but she made no continuous studies of the respiration during dormancy, while in germinative conditions. The development of continuous reading respirometers has made it possible to follow the respiratory changes hour by hour, day by day, for long periods. A new design of this type of respirometer is described in this paper.

The work here reported was undertaken to determine the respiration behavior of the upper seeds of *Xanthium* during long periods in the germinators, and to correlate changes in the weight of the seeds during these periods with the CO_2 losses in respiration.

Methods

In order to standardize the conditions of experimentation, the following procedure was adopted. The seeds were kept under constant temperature and moisture conditions at atmospheric pressure, in a Freas thermostat. The seeds were protected from yeasts or other microorganisms by careful handling, but otherwise unsterilized, as some sterilizing agents, like 10 per cent Javelle water, seemed to modify the behavior. At regular intervals the respiration rate was determined, and also weight changes for seeds kept under the same conditions.

The excellent respirometers which have been designed by other workers are not convenient for continuous readings, so an apparatus has been devised for this type of investigation (fig. 1). This consists of three parts, a respirometer chamber, an air tank, and a water manometer. The bulb (*A*) is a respiratory chamber, which is made from a small lamp chimney. This is connected with a storage

bottle (*B*) for sodium hydroxide solution by means of a large rubber tube. This bottle is made from a gooch filter tube, and connected with a short rubber tube to an outlet, which is drawn to a

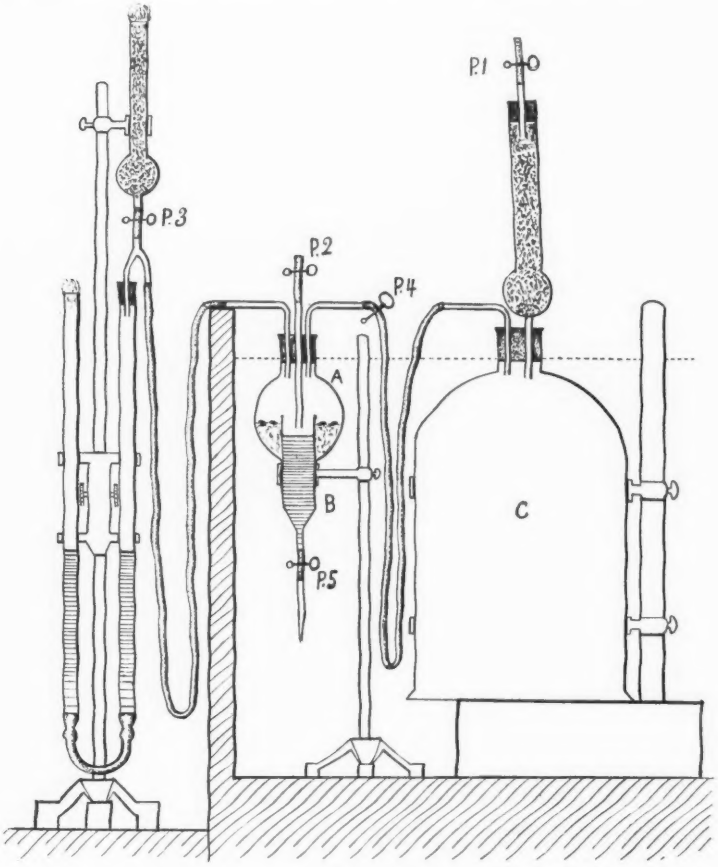

FIG. 1.—Respirometer apparatus.

small opening. The respiratory chamber is also connected by means of tubes to the air tank (*C*) and the leveling water manometer, made of two burettes connected by tubing. The air chamber is made from a large belljar, protected by a soda lime tube, and the burette

manometer was also protected in the same way, as shown in the figure.

The details of the procedure are as follows. The apparatus is first sterilized with formalin solution, and washed with sterilized water. Then the air tank is placed in the water bath, while the pinch clamp (P_1) is opened, to drive out the air by water pressure. The tank full of water is now lifted until the lower edge of the belljar is a short distance beneath the surface of the bath. By opening the pinch clamp very slightly, a slow current of CO_2-free air is brought into the belljar until it is partially or nearly filled, after which the tank is fastened down securely in the water bath.

The seeds are introduced into the respiratory chamber, and placed on wet absorbent cotton which surrounds the neck of the storage bottle. Opening pinch clamps P_3 and P_2, a normal solution of NaOH is introduced into bottle B by a pipette discharging through the tube closed by P_2. Carbon dioxide-free air from the air tank can be introduced into the respiratory chamber before charging the bottle with NaOH, by opening clamps P_2, P_3, and P_4. The respirometer is then placed in the Freas water bath, the temperature of which was kept at 25° C. during the experiments. After any desired interval, the solution of NaOH can be forced from the bottle into a receiving flask through the outlet tube by opening P_5 and P_4. The water pressure in the air tank, which needs to be only slight, forces the NaOH out of B, and simultaneously introduces CO_2-free air into the respiratory chamber. Any CO_2 which has not yet been absorbed by the solution in B can be swept into the absorbing solution by keeping the pointed end of the delivery tube beneath the surface of the solution in the receiving flask while CO_2-free air recharges the respiration chamber.

The water manometer is used to adjust the air pressure of the respiration chamber to atmospheric conditions by opening P_3, after which all pinch clamps are closed. Any change of level after the clamps are closed serves as a rough indicator of respiration. It really indicates the amount of oxygen absorbed during the interval. The amount of CO_2 evolved in any given interval is determined by the double titration method used by BROWN and ESCOMBE (2) some years ago.

The *Xanthium pennsylvanicum* seeds used were collected at Homewood, Illinois, at the close of the winter season early in 1924. The greatest possible care was used in removing seeds from the burs, so as not to injure the seed coats, and to keep them clean and free from infection. As some sterilizing agents seemed to influence germination behavior, particularly the 10 per cent Javelle water, it was decided not to sterilize the seeds for fear that coat or embryo characters might in some way be affected by the treatment. By careful handling it was relatively easy to avoid any kind of yeast or mold growth, and since the seeds were removed from the burs only immediately before using, bacterial infections were not difficult to avoid.

Results

The experiments were repeated several times, and always with consistent results. In some cases the seeds were soaked in water in

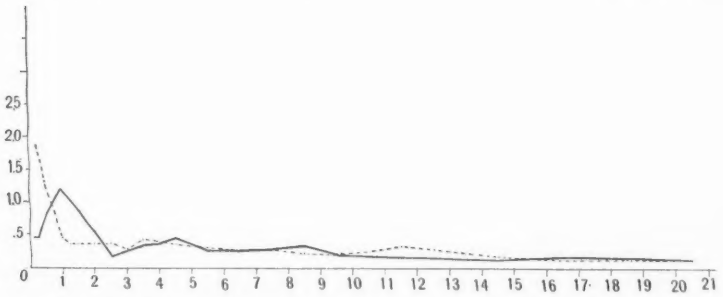

FIG. 2.—Respiration of upper seeds in respirometers: horizontal axis represents time in days, vertical axis represents mg. of CO_2, continuous line represents unsoaked seeds, broken line represents soaked seeds.

an icebox over night previous to placing them in the respirometer, while in other cases they were introduced into the respirometer dry, so that soaking occurred on the wet absorbent cotton in the chamber. The experiments were run for three weeks each. While this is a relatively short period, it is clear from the consistent behavior of the seeds that the course of respiration would continue indefinitely along the lines noted during the last two weeks of this period.

The data for the respiration of unsoaked seeds are shown in table I, and for soaked seeds in table II. Both results are shown graphically in fig. 2.

TABLE I

RESPIRATION OF UNSOAKED XANTHIUM SEEDS

TIME IN HOURS	CO_2 GIVEN OFF BY 20 SEEDS (MG.)	CO_2 GIVEN OFF BY 20 SEEDS PER HOUR (MG.)	NO. OF GERMINATIONS
0–4	1.7600	0.4400	
4–8	1.7600	0.4400	
8–13	3.5200	0.7040	
13–24	13.2000	1.2000	
24–36	8.8000	0.7333	
36–48	6.1600	0.5133	
48–60	2.2000	0.1833	
60–72	2.6400	0.2200	
72–84	3.9600	0.3300	
84–96	4.4000	0.3667	
96–108	4.8400	0.4033	
108–132	6.6000	0.2750	
132–156	6.6000	0.2750	
156–180	6.6160	0.2757	
180–204	7.4800	0.3117	1
204–228	5.0600	0.2108	
228–252	4.6200	0.1925	
252–276	4.1480	0.1728	
276–300	3.6859	0.1536	
300–348	6.6000	0.1375	
348–396	7.920	0.1650	1
396–444	7.040	0.1467	
444–492	6.600	0.1375	

TABLE II

RESPIRATION OF SOAKED XANTHIUM SEEDS

TIME IN HOURS	CO_2 GIVEN OFF BY 20 SEEDS (MG.)	CO_2 GIVEN OFF BY 20 SEEDS PER HOUR (MG.)	NO. OF GERMINATIONS
0–6	11.0000	1.8333	
6–12	4.8400	0.8067	
12–24	5.2800	0.4400	
24–30	2.2000	0.3667	
30–36	2.2000	0.3667	
36–48	4.4000	0.3667	
48–60	4.2000	0.3500	
60–72	3.5200	0.2933	
72–84	4.8400	0.4033	
84–108	8.8000	0.3667	
108–132	7.0400	0.2933	
132–156	7.0400	0.2933	
156–180	6.6000	0.2750	
180–204	5.2800	0.2200	
204–228	4.8400	0.2017	
228–252	6.1600	0.2567	
252–276	7.4800	0.3117	1
276–300	7.0400	0.2933	
300–348	9.2400	0.1925	
348–396	7.4800	0.1558	
396–444	7.2000	0.1500	
444–492	6.6000	0.1375	

It is seen from the tables and graphs that the respiration rate rises rapidly during the first day or so of germinative conditions, reaching a maximum during this brief period. After this initial

TABLE III

RESPIRATION AFTER REDRYING AND WEIGHT LOSS

TIME (HOURS)	CO_2 GIVEN OFF BY 20 SEEDS (MG.)	CO_2 GIVEN OFF BY 20 SEEDS PER HOUR (MG.)	DRY WEIGHT OF 20 SEEDS (MG.)
0–6	4.4000	0.7333	946.0 (initial weight)
6–12	7.0400	1.1733	
12–24	8.8000	0.7333	
24–30	4.8400	0.8067	
30–36	3.5200	0.5867	
36–48	3.0800	0.2567	
48–60	3.0800	0.2567	
	Total.. 34.7600	Average. 0.5793	
60–108	seeds dried to air dry weight		870.0
108–114	2.4720	0.4620	
114–120	4.0900	0.6817	
120–132	6.0060	0.5005	
132–138	3.8000	0.6333	
138–144	3.0800	0.5133	
144–156	3.2300	0.2692	
156–168	3.1700	0.2642	
	Total.. 25.8480	Average. 0.4341	
168–216	seeds dried to air dry weight		845.0
216–222	2.8600	0.4767	
222–228	4.4000	0.7333	
228–240	3.9600	0.3300	
240–246	1.9800	0.3300	
246–252	3.5000	0.2917	
252–264	3.9600	0.3300	
264–276	3.0800	0.2567	
	Total.. 23.7400	Average. 0.3957	
276–324	seeds dried to air dry weight		822.3

increase the respiration rate falls rapidly, with some slight fluctuations during the second and third days, to a low level, after which there is a very slow decrease in rate as long as the experiment is continued.

The graphs also show clearly that the soaked seeds reach their maximum respiration rate much sooner than dry seeds. It only takes about 6 hours for the soaked seeds, but 12–24 hours for the dry seeds to reach the point of most rapid evolution of CO_2. If at any time a seed germinated unexpectedly, there was always a corresponding increase in the respiration. Such seeds were removed from the respirometer as soon as detected.

The effect of redrying upon the respiration rate was tested. After the seeds had reached the low level of respiration in the respirometer, they were removed and dried, and then used again for an experiment. It was thought that they might again show an

TABLE IV

RESPIRATION AND WEIGHT LOSS IN XANTHIUM SEEDS

No. of lot (10 seeds)	Initial dry weight (gm.)	Time in hours	Decrease in weight	Decrease in wt. per gm.
1	0.3309	6	0.0108	0.0326
2	0.3640	12	0.0168	0.0462
3	0.4127	18	0.0197	0.0478
4	0.5528	24	0.0368	0.0666
5	0.4080	36	0.0320	0.0784
6	0.3711	48	0.0321	0.0865
7	0.4240	144	0.0340	0.0800
8	0.3903	288	0.0370	0.0874
9	0.3720	480	0.0386	0.1038

initial high respiration rate. The results of tests are given in table III and fig. 3, which show that the expected initial rise in respiration can be obtained repeatedly by redrying and subjecting to germinative conditions.

The weight changes accompanying long continued respiration of dormant seeds have been followed in five series of experiments, which were frequently disturbed by the unexpected germination of seeds. The results shown in table IV and fig. 4 are compiled from three series of tests. The initial weight is taken as the air dry weight, but in determining the loss in weight the seeds were oven dried at 103° for 5 hours after drying at room temperature for 24 hours.

The general result shows a relatively rapid decrease in weight during the first several days, but after this the rate decrease is slow,

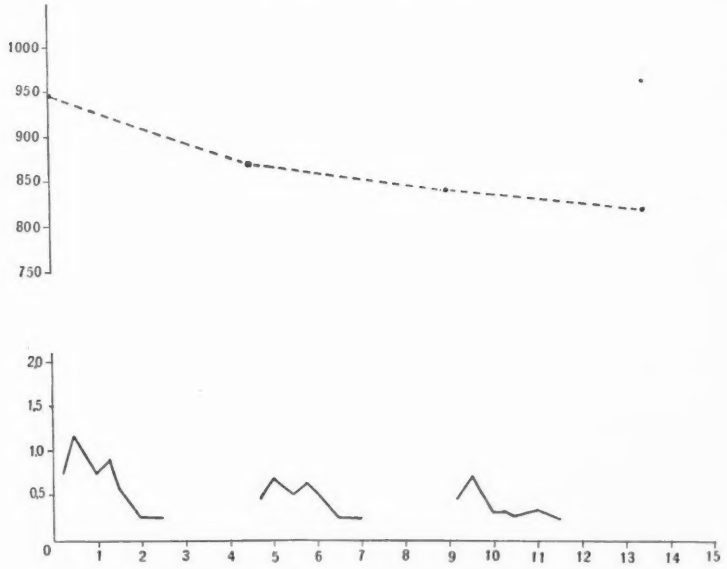

FIG. 3.—Respiration of redried seeds: horizontal axis represents time in days, vertical axis represents weight in mg., continuous line represents respiration rate, broken line represents weight change.

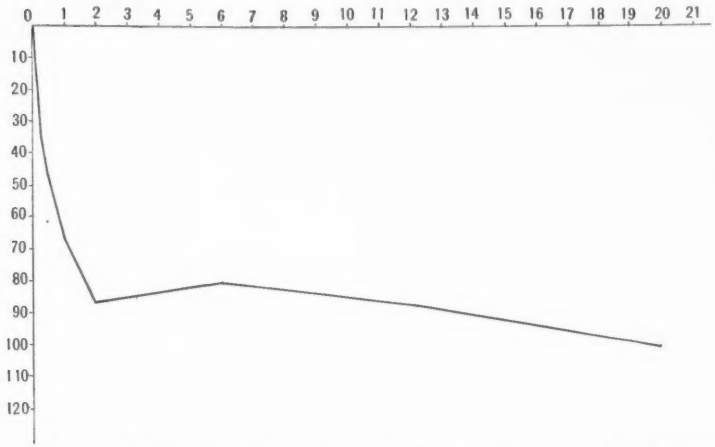

FIG. 4.—Weight changes of upper seeds: horizontal axis represents time in days, vertical line represents decrease of weight in mg. per gram of seeds.

corresponding to the slow respiration rate as determined from CO_2 evolution.

Discussion

As was mentioned in the introduction, a study of respiration of dormant seeds was made by Miss SHERMAN (**5**), who determined experimentally the respiratory intensity, that is the mg. CO_2 eliminated per gram of imbibed seeds per hour for *Amaranthus retroflexus*, *Chenopodium album*, and *Rumex crispus*, as well as for *Crataegus* and certain drupaceous Rosaceae. Her data show that the amount of CO_2 evolved per gram of imbibed weight per day at 25° C. is between 1.548 and 4.213 mg. for these seeds. The respiratory intensity varies markedly for different kinds of seeds. She made no studies of *Xanthium* seeds, and in no case were the seeds studied continuously while in germinative conditions. The work here reported, therefore, is not directly comparable with Miss SHERMAN'S work, as it deals with a somewhat different phase of respiratory behavior, the long continued respiration of dormant seeds kept in conditions otherwise suitable for germination.

These experiments show that the dormant upper seeds of *Xanthium* show a high respiration rate during the first few days. If the data of the first 60 hours of table III are taken, the amount of CO_2 eliminated per gram of dry seeds per 24 hours at 25° C. is 14.48 mg., but if the data at the twentieth day be taken, the evolution of CO_2 is only about one-tenth as great.

Many plant and animal physiologists have found a parallelism between catalase activity and respiratory intensity. Miss SHERMAN, however, found instances in which there was no direct correlation between these two activities. Fluctuations in the two did not occur simultaneously, and might be in opposite directions. More recently, Mrs. RHINE (**4**) has found that respiratory and catalase activity go in opposite directions in the earliest stages of germination in all the types of seeds tested.

In the experiments of SHULL and DAVIS it was found that the upper seeds of *Xanthium* showed increased catalase activity during the first two days in the germinator, but as the period of exposure lengthened, the activity decreased to less than one-third at 43 days, and at 93 days was no greater than in seeds kept in air dry storage.

When a seed was broken and began to germinate after 42 days, the catalase activity increased suddenly.

Inspection of the respiration curve in fig. 2 shows that the respiration behavior in the respirometer is very similar to the catalase behavior in the germinator. In these later stages, it is certain that the catalase activity and respiratory activity run closely parallel throughout the period of dormancy.

The fact that the respiration rate of soaked seeds reached its maximum in the respirometer earlier than that of unsoaked seeds, is mainly due to the fact that the unsoaked seeds needed time to take in sufficient water for destructive metabolism, while soaked seeds have already imbibed sufficient water for this purpose. It is well known that the dry weight of ordinary seeds decreases rapidly during germination, while respiratory activity increases. In the case of dormant seeds the same relations exist; if respiratory activity is rapid, weight loss is rapid; when the respiration is slow, weight decrease is slow. Calculations based on the data presented show a more rapid weight loss than actually occurs in long time experiments, which can only mean that the respiratory loss and weight loss continue to decline until the daily loss is insignificant. Even if the twentieth day rate of respiration is taken, the evolution of CO_2 found would be sufficient to exhaust the carbon of the seed in a couple of months, counting the seed 50 per cent carbon. They have been kept in germinators for 93 days without exhausting the reserve food, however, and in nature must be able to withstand at least several years of slow respiration without complete exhaustion of the food carbon.

Summary

1. There is a notable increase in the respiration rate of dry seeds during the first day of subjection to favorable germinative conditions in the respirometer.

2. After this initial increase, the respiration rate falls rapidly, with some slight fluctuations during the second and third days, to a low level, after which there is a very slow decrease in rate as long as the experiment is continued.

3. If the seeds are soaked in cold water previous to placing them in the germinator, the respiration rate reaches its maximum earlier

than unsoaked seeds; otherwise the curve of respiratory activity is the same as in unsoaked seeds.

4. If the seeds are taken from the respirometer and dried, and again placed in the respirometer, they always show the increased respiration immediately after being placed in germinative conditions.

5. The weight changes occurring in seeds during long periods of dormant respiration have also been noted and compared with the respiration data. The experiments did not run long enough to give the natural rate of carbon loss from respiration in nature.

6. Respiratory activity and catalase activity in these seeds run parallel throughout the period of dormancy.

The writer desires to express his appreciation and gratitude to Professor CHARLES A. SHULL, under whose direction these experiments were carried on, and to Dr. S. V. EATON for many suggestions during the course of the work.

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NOTES ON THE "SPRUCE BUDWORM" BIOCOENOSE

II. STRUCTURAL ABNORMALITIES IN ABIES BALSAMEA

I. W. Bailey

(WITH PLATES XIII–XV AND THREE FIGURES)

Introduction

As noted in the first paper of this series,[1] analyses of the growth rings in the stems of spruce and fir balsam have afforded useful criteria in studying the activities of the budworm, *Cacoecia fumiferana*, in the coniferous forests of Eastern Canada. In the case of the fir balsam, the problem of accurately dating the layers formed during specific growing seasons is complicated by the occurrence of dark reddish brown zones, which tend at times to simulate the outer boundaries of true growth layers. It is essential to determine whether these apparent abnormalities are induced by the feeding of the budworm, and to obtain more reliable information concerning their significance in stem analyses.

Macroscopic investigation

In transverse sections of normal, uninjured stems of fir balsam, the two or three innermost growth layers (those next to the pith) are characterized by having a more or less intensified, dark reddish brown color. The "discoloration" may be diffused throughout the growth layers, confined to broad zones in their outer portions, or distributed sporadically in irregular patterns. It becomes evanescent in the three or four succeeding growth layers, and disappears in subsequently formed tissue.

In sections of fir balsam which have been attacked by the budworm, there are at times two or three sharply defined, narrow, dark reddish brown zones. These discolorations are not restricted to the innermost growth layers, however, but may be present in various portions of the tissue differentiated during the first 8–12 growing seasons. An examination of series of transverse sections, from differ-

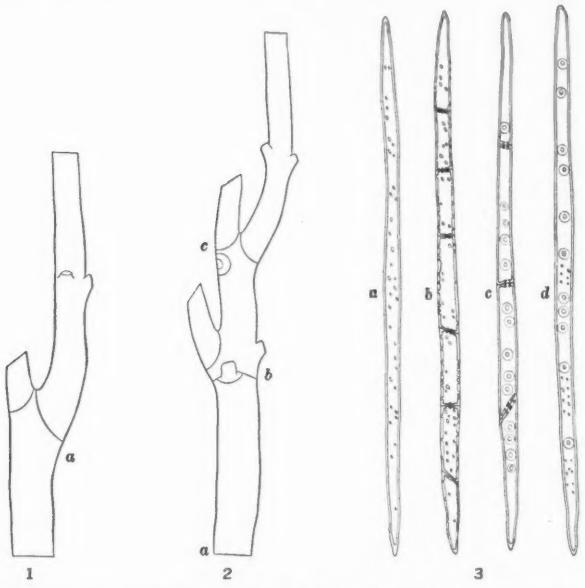
[1] Bot. Gaz. 80: 93–101. 1925.

ent levels of the cauline axis, reveals the fact that discolorations of this type are confined to the upper extensions of growth layers, formed subsequent to the advent of the budworm. This, of course, suggests that they are induced either directly or indirectly by the feeding of the insects. In most cases the defoliating activities of the budworm extend over a period of from two to four years. Each season the young larvae feed upon the tender, recently formed leaves, and subsequently consume a varying proportion of the older foliage. Thus the injurious effects of defoliation tend to be intensified in the terminal shoots. That the formation of the narrow, zonal discolorations is more or less closely correlated with injuries to the apical shoots, is indicated by a detailed investigation of such specimens as those illustrated in text figs. 1 and 2. The terminal shoot in text fig. 1 was severely injured by the feeding of the budworm, and subsequently was replaced by a lateral shoot which curved upward into a vertical position. Fig. 4 is a transverse section of the stem cut at level *a*. The narrow, innermost layer is jacketed by two broad growth rings of normal, circular outline. The succeeding ring also is cylindrical, but is much reduced in width. The six outer layers are strikingly eccentric, and are characterized by having conspicuous arcs of so-called compression wood or Rotholz. HARTIG[2] and others have shown that this type of eccentricity is closely correlated with the upward bending of lateral shoots. It is evident, therefore, that the abnormally narrow, cylindrical growth layer in fig. 4 must have been formed during the growing season in which the injury to the apical shoot occurred. This layer has a narrow, dark reddish brown zone of discoloration close to its outer margin. The discoloration is visible in sections from a number of successively lower levels. In other words, it has a considerable longitudinal extension below the stub of the terminal shoot. It should be noted, in this connection, that its upper portions are closer to the pith than are its basal extensions. This, of course, is due to the fact that the layer, to which it is confined, jackets an increasing number of previously formed growth rings at successively lower levels.

In the specimen illustrated in text fig. 2, there are evidences of

[2] HARTIG, R., Holzuntersuchungen: Alters und Neues. Berlin: J. Springer. 1901 (pp. 46–99).

three successive injuries to shoots in the apical portions of the stem. The differentiating terminal and lateral shoots at level *b* were severely injured during the first year (1914) of feeding of the budworm. The apical shoot survived this attack, but was so severely injured during the succeeding growing season that it was replaced



FIGS. 1–3.—Fig. 1, terminal portion of stem of fir balsam seriously injured by defoliation in 1914; during the 1915 growing season a lateral shoot curved upward to replace injured terminal shoot; fig. 2, apical portion of stem of fir balsam, showing successive malformations due to feeding of budworm; fig. 3, types of cells formed by fusiform initials of cambium: *a*, simple pitted, unsegmented parenchymatous derivative; *b*, simple pitted, segmented parenchymatous derivative; *c*, septate tracheid; *d*, normal, unsegmented tracheid.

by one of the laterals, level *c*. Less conspicuous malformations were produced in the following year. Fig. 3 is a transverse section of this stem cut at level *a*. There is a narrow zone of discoloration in each of the 1914–1916 growth layers. As in the preceding specimen, these discolorations, which have a considerable longitudinal extension, are confined to growth layers formed during seasons in which injuries to the apical shoots occurred.

Microscopic investigations

As shown in figs. 5–7 and figs. 9–12, the dark reddish brown discolorations are due to the presence of cells which contain an amber colored substance (appearing black in the photomicrographs). In the case of the broader, less symmetrical discolorations, that is, those which are not confined to growth layers formed subsequent to the advent of the budworm, these "resin" cells are more or less widely and irregularly scattered (fig. 5). On the contrary, in the case of the discolorations which are correlated with injuries to the apical shoots, they are aggregated in relatively narrow zones (figs. 6, 7, 10, 11, 12), and not infrequently are associated with traumatic "resin" cysts (figs. 6, 7, 10, 12).

Two types of vertically elongated, "resin"[3] bearing cells are known to occur in the secondary wood of the Coniferales, resinous tracheids and resiniferous wood parenchyma. The former are normal tracheids into which resinous material is supposed to have diffused from the adjoining ray parenchyma. The "resin" occurs in the form of more or less massive, biconcave, transverse septa. Such resinous cells are considered characteristic features of the wood of certain representatives of the Cordaitales and araucarian conifers, but may occur at times in *Abies* and *Pinus*, as PENHALLOW[4] and RECORD[5] have shown. Wood parenchyma is present in many of the higher gymnosperms. In certain plants it tends to be confined to the outer surface of the so-called summer wood, whereas in others it is more or less regularly diffused throughout the secondary wood. In the cells of this tissue, the resinous material, which varies greatly in form and color, is presumably *in situ*.

In the case of the discolorations which occur in the inner growth layers of normal, uninjured fir balsams, the resin bearing elements appear at first sight to be tracheids. This is due to the fact that they are of similar size and form, and that their pitting is obscured by

[3] The words resin, resinous, resiniferous, etc., frequently are used in referring to substances of unknown chemical composition. Many of these amber colored substances do not exhibit the typical reactions of true resins.

[4] PENHALLOW, D. P., A manual of the North American gymnosperms. Boston: Ginn & Co. 1907. pp. 53–58.

[5] RECORD, S. J., Significance of resinous tracheids. BOT. GAZ. 66: 61–67. 1918.

their amber colored contents. A detailed study of their secondary membranes, however, shows them to be provided with small, simple openings (text fig. 3 and fig. 17) instead of with large circular bordered pits. The occurrence of such cells in the secondary xylem of the gymnosperms, so far as the writer has been able to determine, is unique. It raises the question whether they should be designated as resinous libriform fibers, as resinous substitute fibers, or as structures *sui generis*.

In the narrow zones of discolored tissue which are confined to growth layers formed subsequent to the advent of the budworm, these cells occur in association with normal tracheids (fig. 13), septate tracheids (fig. 14), resiniferous wood parenchyma (fig. 15), or traumatic resin cysts (fig. 16). In general, the amber colored substance is confined to elements having simple pits, and, in most cases at least, does not diffuse into the tracheary cells. In other words, the cambium forms two distinct categories of vertically elongated cells, tracheids and simple pitted elements which tend to remain physiologically active during a longer period and to secrete an amber colored substance. Both types of cells are derived from the same fusiform cambial initials. Furthermore, in both categories of elements, the fusiform daughter cells of the cambium may divide transversely before differentiating into bordered pitted or simple pitted elements (text fig. 3). It is significant, in this connection, that the frequency of such transverse divisions appears to vary directly with the quality or the intensity of the traumatic stimulus. For example, septate tracheids and resin bearing cells in close proximity to "resin" cysts tend to be composed of short segments, whereas the outlying cells are nonseptate or exhibit two or three transverse divisions.

Such facts suggest that the simple pitted cells in the innermost rings of normal, uninjured fir balsams are essentially parenchymatous, and may be designated as nonseptate or unsegmented wood parenchyma. Their resemblance to tracheary elements is due to the fact that both types of cells are derived from fusiform cambial initials, and therefore are of similar form. It should be emphasized in passing that the significance of the shape of the cambial initials has been overlooked in phylogenetic speculations concerning the origin of wood parenchyma. For example, the fact that series of

vertically contiguous parenchymatous cells have a fusiform outline, resembling that of tracheary elements, has been advanced as indicating that wood parenchyma is primitively derived from modified tracheids. Such an assumption, of course, is entirely unjustifiable. Nor is the occurrence of short tracheids in association with parenchymatous elements necessarily indicative of the derivation of wood parenchyma from septate tracheids. There is an evident tendency toward the replacement of tracheary by parenchymatous elements in the secondary xylem of many of the higher gymnosperms, but there is no reliable evidence of an evolutionary metamorphosis of tracheids into wood parenchyma, that is, that tracheids became septate and subsequently lost their bordered pits and reacquired living contents. Even in the case of the dicotyledons, it is a question whether the so-called substitute fibers actually are modified tracheary elements, or are elongated, thick walled, unsegmented wood parenchyma.

As shown in figs. 13–17, the amber colored substance in the parenchymatous elements of fir balsam occurs in various granular, alveolar, and more or less massive forms. It not infrequently appears as an inner jacketing layer with numerous transverse septa of varying width (fig. 13). The more massive, biconcave septa (figs.13–15) closely resemble those that occur in the resinous tracheids of the Cordaitales and Araucarieae. The tenuous types (figs. 13, 17) give to the elements in which they occur the appearance of being divided into short segments.

Significance of reddish brown discoloration in stem analyses

Although the narrow, zonal discolorations are of considerable value in distinguishing tissue formed subsequent to the advent of the budworm, in many cases they are serious obstacles in studying the chronology of the successively formed growth layers. This is due to the fact that, when they are formed at the end of the growing season, they tend to obscure the outer margin of the growth ring, and, when they are differentiated earlier, they tend to divide the growth ring into two apparently distinct layers. The difficulties in distinguishing the outer margins of true growth layers, of course, are considerably accentuated in macroscopic analyses, but cannot in all

cases be overcome by a microscopic examination of specific transverse sections.

In fig. 7, the inner growth layer terminates in a zone of narrow tracheids, which is subtended by a conspicuous zone of traumatic tissue. There is an inner zone of diffusely scattered "resin" cells, which are associated with enlarged tracheids. All of this tissue was formed during a single growing season (1911), and there is no uncertainty concerning the interpretation of its principal topographical features. The same thing is true of the inner (1911) growth layer in fig. 6. It terminates in a conspicuous zone of summer wood, which is subtended by a zone of aggregated wood parenchyma. The succeeding tracheary tissue is divided into two portions by a narrow zone of traumatic "resin" cysts and "resin" cells. There is a slight tendency toward a reduction in the width of the tracheids in the vicinity of this zone of discolored tissue, but there is no reliable structural evidence to indicate whether the zone of discoloration was formed during or at the end of the growing season. Similar difficulties are encountered in interpreting the structures in figs. 11 and 12.

It occurred to the writer that it might be possible to overcome such uncertainties by tracing the zones of discoloration downward into the level of the stem at which they disappear. At their lower extremities, the outer zones of traumatic tissue in figs. 6 and 12 grade into conspicuous zones of summer wood. On the contrary, the outer of the two central zones of traumatic "resin" cells in fig. 11 fades away in what appears to be the inner portion of a growth layer, and is not subtended longitudinally by a zone of dense tissue. This suggests that the zonal discolorations in figs. 6 and 12 were formed at the end of the growing season, and therefore coincide with the outer margins of true growth layers; but that one of the putative layers in fig. 11 is a false ring. It should be emphasized, however, that the occurrence of tracheids of reduced radial width in fig. 11 raises the question whether the dense layers which subtend the outer discolorations in figs. 6 and 12 are false zones of summer wood induced by the feeding of the budworm. The question may be answered by accurately dating the growth layers, for example, by the method outlined in the first paper of this series. In

the specimens illustrated in figs. 6 and 12, there is one layer for each of the 1911, 1912, and 1913 growing seasons. On the contrary, in fig. 11 the 1917 growth ring is divided into two apparently distinct layers.

A detailed study of a large number of fir balsams from various forest areas in western and south central Quebec, and from northern New Brunswick indicates that broad, conspicuous "false" layers of summer wood are of rare occurrence in trees attacked by the budworm. When present, they rarely extend around the entire circumference of the stem, and are of much restricted longitudinal distribution. Thus, they do not present a serious practical obstacle in stem analyses. Of greater significance is the fact that cambial activity may be arrested during one or more growing seasons, particularly in the median and basal portions of the cauline axis. A reduction in the number of layers, therefore, in passing from a higher to a lower level of the stem, may be due to the presence of a false ring (fig. 11) at the former level, or to the omission of a growth layer at the latter level. It should be noted in this connection, however, that if the two 1917 layers in fig. 11 were distinct annual rings, one of which disappeared at a lower level, the dividing zone of traumatic tissue would not terminate in the central portion of a growth layer. If the inner layer became evanescent at lower levels, its outer margin would gradually approach that of the preceding ring. Similarly, if the outer layer faded away at lower levels, its outer margin would approach the zone of tissue in which the discoloration occurs.

It is evident, therefore, that there are two methods of studying the chronology of the growth layers in stems of fir balsams that have been attacked by the budworm: (1) by using frost rings as indicators, and (2) by carefully tracing the growth layers and the zones of discolored traumatic tissue downward into successively lower levels of the stem. The former method necessitates an extensive preliminary examination of the distribution of frost injuries in the vegetation of specific forest areas; the latter involves a careful dissection of the cauline axis, particularly of its slender, upper portion. Either method may be used in the case of trees which have recovered from the attacks of the budworm. In the case of trees which

have been killed by defoliation, or of dying trees in which the date of formation of the outermost ring is not accurately known, both methods are essential.

Structural abnormalities produced by Pissodes dubius

The weakened and dying trees in coniferous forests which have been defoliated by the budworm are attacked by various insects and fungi. One of the commonest of these secondary parasites is *Pissodes dubius*. The adult weevils bore into the stems of fir balsam and feed upon the inner phloem and cambium. In so doing, they excavate shallow, oval cavities which later may become more or less completely occluded by wound tissue (fig. 2). If the bark is removed from the stems of trees which were attacked by the weevils during the preceding growing season, the surface of the woody cylinder will be found to be covered with narrow, vertically elongated, dark reddish brown streaks. These discolorations originate in the vicinity of the injuries produced by the feeding of *Pissodes*, and extend a considerable distance above and below them. As indicated in figs. 1 and 8, they are due to the presence of traumatic "resin" cysts whose epithelial cells contain an amber colored substance.

The feeding scars and associated discolorations are of such characteristic form and distribution, that they may be utilized in tracing the former activities of the weevils in different regions. For example, in the case of trees which have fully recovered from the effects of the earlier outbreaks of the budworm (1909, 1910, 1911, etc.), the occurrence of these abnormalities in the narrower growth layers, formed subsequent to the advent of the budworm, indicates that the trees were attacked by *Pissodes* before they recovered from the effects of defoliation. Similarly, in the case of dead and dying trees, it is possible to determine the dates of the growing seasons during which the weevils were actively feeding upon the trees.

Summary

1. In transverse sections of the stems of fir balsams that have been attacked by the spruce budworm, there frequently are two or three narrow, dark reddish brown zones of discolored tissue.

2. These discolorations are due to the presence of parenchy-

matous elements which contain an amber colored substance. They are confined to the upper extensions of growth layers formed subsequent to the advent of the budworm, and are induced by injuries to the terminal shoots.

3. The abnormalities not infrequently are serious obstacles in studying the chronology of the successively formed growth layers of the cauline axis. Two methods of overcoming such difficulties in stem analyses are briefly outlined.

4. The weakened and dying trees in coniferous forests that have been defoliated by the budworm are attacked by various insects and fungi. One of the commonest of these secondary parasites is *Pissodes dubius*. It is shown that the areas of traumatic tissue induced by the feeding of this weevil are of considerable significance in stem analyses.

The data presented in this paper were collected during a reconnoissance for the Entomological Branch of the Canadian Department of Agriculture.

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DESCRIPTION OF PLATES XIII–XV

Fig. 1.—Transverse section of outer growth layers of old stem, showing arc of traumatic "resin" cysts induced by feeding of *Pissodes dubius;* first feeding of budworm in 1918; ×15.

Fig. 2.—Transverse section, showing scar due to feeding of *Pissodes dubius;* ×25.

Fig. 3.—Portion of transverse section, cut at level (*a*) (text fig. 2); first feeding of budworm in 1914; ×15.

Fig. 4.—Transverse section, cut at level *a* (text fig. 1); first feeding of budworm in 1914; ×5.

Fig. 5.—Transverse section of wood in close proximity to pith, showing diffusely scattered, dark parenchymatous elements; ×30.

Fig. 6.—Transverse section of 1912 and of portions of 1911 and 1913 growth layers, showing zones of aggregated parenchymatous elements and "resin" cysts; first year of feeding of budworm 1911; ×30.

Fig. 7.—Transverse section of portions of 1911 and 1912 growth layers, showing zones of aggregated parenchymatous cells and "resin" cysts; first year of feeding of budworm 1911; ×30.

FIG. 8.—Transverse section of wood, showing traumatic "resin" cysts induced by feeding of *Pissodes dubius;* ×40.

FIG. 9.—Transverse section of outer boundary of growth layer, showing loosely aggregated parenchymatous elements; ×50.

FIG. 10.—Transverse section of 1914 and 1915 growth layers, showing zones of aggregated parenchymatous elements and "resin" cysts; first feeding of budworm in 1914; frost injury at *f;* ×15.

FIG. 11.—Transverse section of 1916 and 1917 growth layers, showing zone of aggregated parenchymatous elements which appears to divide the 1917 ring into two distinct layers; ×30.

FIG. 12.—Transverse section of 1911, 1912, and 1913 growth layers, showing distribution of parenchymatous elements and "resin" cysts; first year of feeding of budworm 1911; ×25.

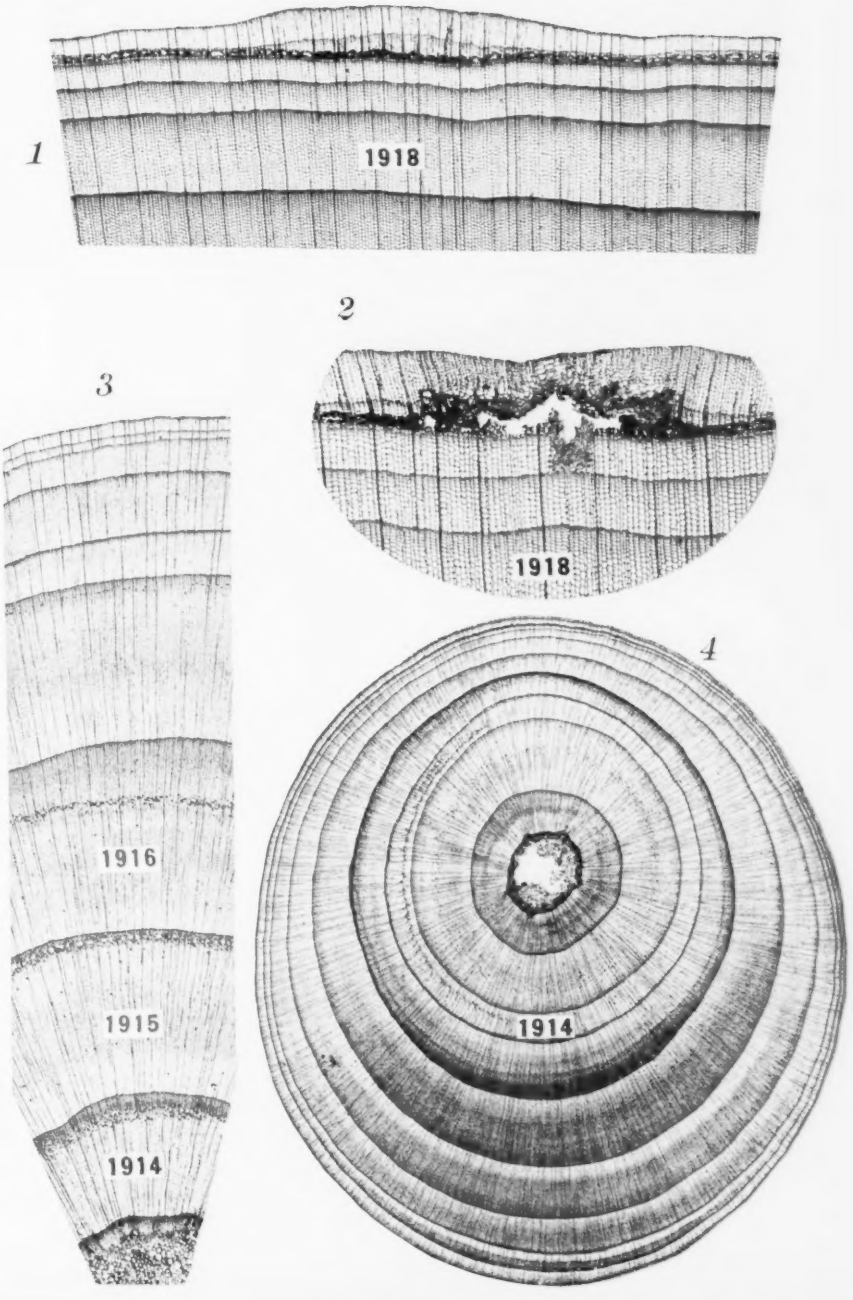
FIG. 13.—Tangential longitudinal section, showing various forms of amber colored substance in unsegmented wood parenchyma; ×65.

FIG. 14.—Tangential longitudinal section, showing various forms of amber colored substance in unsegmented wood parenchyma; note presence of septate tracheids; ×87.

FIG. 15.—Tangential longitudinal section, showing septate and non-septate wood parenchyma; ×120.

FIG. 16.—Tangential longitudinal section of tissue in close proximity to "resin" cyst, showing parenchymatous cells and septate tracheids; ×120.

FIG. 17.—Radial longitudinal section: *a*, tracheid with large bordered pits; *b*, unsegmented parenchymatous element with simple pits; *c*, similar cell in which amber colored substance forms tenuous transverse septa; ×400.



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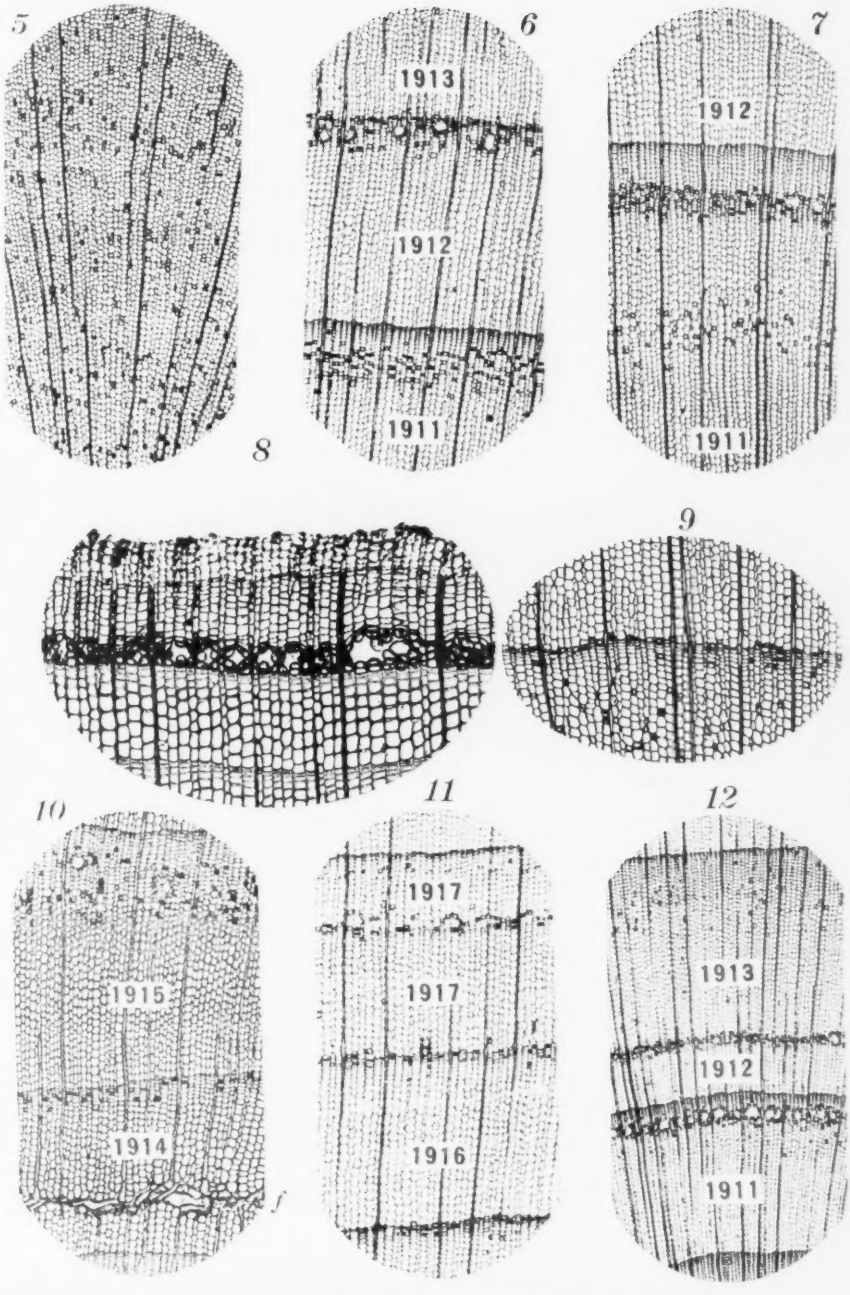

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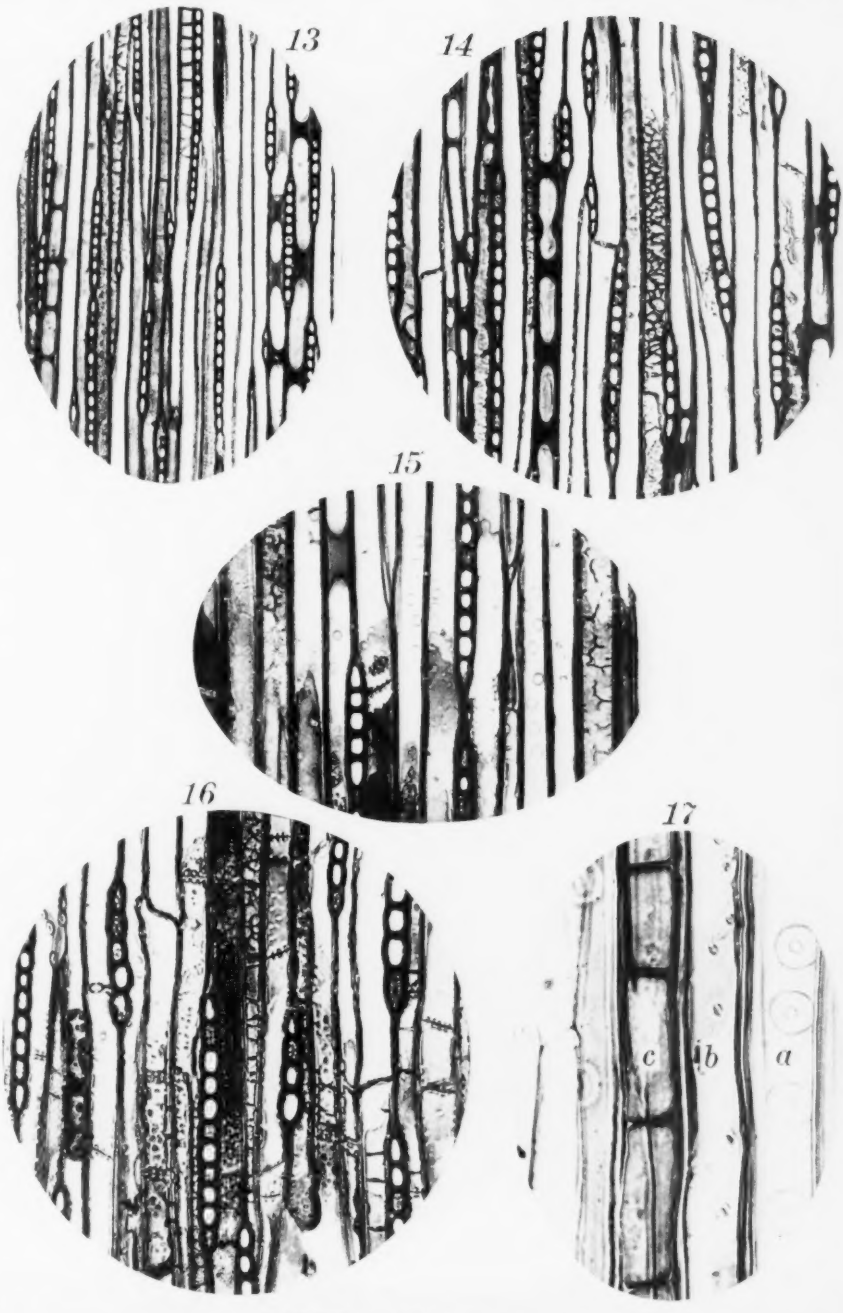

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MORPHOLOGY OF CONIDIOBOLUS VILLOSUS

G. W. MARTIN

(WITH PLATE XVI AND THREE FIGURES)

The fungus described in this note appeared in July, 1923, on a plate of nutrient agar inoculated from a piece of very rotten wood. This wood, collected in a moist thicket on the banks of the Iowa River, was covered with a brown *Hypochnus*, and an attempt was made to secure the latter in pure culture. Other fungi, especially the one here considered, grew so rapidly in the cultures that the attempt was abandoned, and the original collection discarded, before it was realized that the most conspicuous contamination was an undescribed species of *Conidiobolus*. It was readily secured in pure culture, and proved itself capable of developing an extensive mycelium with great rapidity on ordinary nutrient media. On solid media the hyphae are of rather uniform size, averaging 12 μ in diameter and branching rather sparingly. When growing in a liquid medium, variation in size is greater and branching may be profuse. In either instance considerable difference in this respect may be due to the medium. Hyphae immersed in prune decoction, for example, branch much less freely than those growing in a decoction made from fresh green beans (text fig. 1). Growth is vigorous in both instances. As the hyphae grow, the older parts tend to become emptied of protoplasm, and cut off by septa from the protoplasm-filled tip. Frequently a septum appears before the protoplasm is all withdrawn, and in this way numerous segments are isolated, filled with protoplasm, with emptied and shrunken hyphal portions on either side (fig. 8 *c*). If food is abundant, these segments may send out lateral branches almost at once (fig. 20). In old and exhausted or dried cultures they tend to remain dormant and to accumulate, assuming various enlarged shapes, and forming hyphal bodies entirely homologous with the well known structures to which that name is applied, formed by the Entomophthoraceae attacking insects (fig. 19 *a-f*). In the species under consideration, however, these hyphal bodies

for a long time retain something of their mycelial character, to be explained, presumably, by the saprophytic habit.

As soon as the mycelium is well established, numerous conidiophores arise from the substratum. These differ from the hyphae of the mycelium mainly in their erect, aërial habit, and in their strongly positive phototropic reaction. As a rule, a slight and usually one-sided swelling develops in the conidiophore shortly before the discharge of the conidium (text fig. 2). The conidiophore is short when

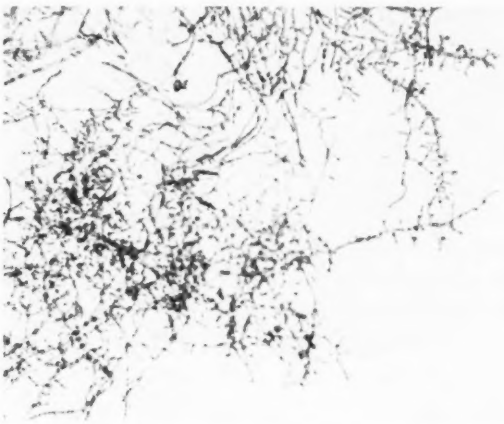

FIG. 1.—Photomicrograph of mycelium developed in bean decoction

growing normally, rarely rising into the air more than twice the diameter of the conidium.

In the formation of the conidium, the protoplasm of the conidiophore flows rapidly into the tip, which swells into a globose mass. When nearly all of the protoplasm has passed into the globose tip, the latter is cut off by a septum. The conidiophore remains turgid, its tip penetrating a short distance into the conidium as a dome-shaped columella. No change occurs for a while, but the protoplasm within the conidium may be observed to be in violent commotion. After some minutes the part of the conidium in contact with the columella is suddenly inverted, forming a short, blunt papilla which presses against the columella; the outer membrane surrounding both conidiophore and conidium is torn, and the latter violently dis-

charged. The maximum vertical discharge observed is over 25 and less than 30 mm., while the lateral distance which the conidia may be thrown, toward the light, is slightly over 30 mm. After the discharge of the conidium, the conidiophore remains turgid for a few minutes, the columella appearing as a swollen tip, with traces of the broken membrane apparent at its base, and either with or without a minute apiculus at its tip (text fig. 2 *b*, *d*, *f*). After a few minutes the conidiophore begins to collapse, and 15 or 20 minutes after the discharge it is shrunken and flaccid (text fig. 1 *e*). The collapse is gradual, not sudden as described by BULLER (**2**) in the

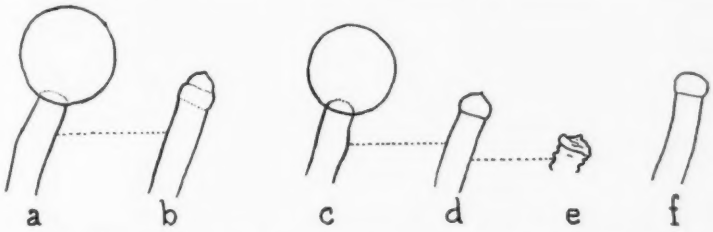

FIG. 2.—Discharge of conidia: *a*, *b*, same conidiophore before and after discharge; *c*, *d*, second type of conidiophore; *e*, collapse of conidiophore shown in *d*, 15 minutes later; *f*, conidiophore without apiculus; all growing in natural position in air on nutrient agar in slide culture.

case of the basidium of an agaric. But one conidium is borne on a given conidiophore.

This account of the discharge of the conidia, based on repeated observation of living material, agrees substantially with the statements concerning the discharge of similar spores, as made by BREFELD (**1**) and OLIVE (**4**). BREFELD, referring to *Conidiobolus utriculosus*, mentions the turgidity of the conidiophore, and describes the discharge as accompanied by a sudden wrench. OLIVE, discussing *Empusa*, particularly *E. sciarae*, basing his account on stained sections, states that "the penultimate cell" (the conidiophore) "forms the explosive mechanism." This is scarcely the case in the species here described. It is true that the conidiophore remains turgid and swollen up to and after the discharge of the conidium, but the active mechanism is the sudden reversal of the basal papilla, due to increasing pressure within the conidium itself.

At room temperature, the conidia are produced in great abundance within 48 hours after a culture is started. They are globose, with the prominent basal papilla characteristic of the family, very variable in size, ranging 12–46 μ in diameter, and averaging about 32 μ (figs. 1, 2; text fig. 3). The smaller dimensions are in general to be attributed to conidia of secondary, tertiary, or a higher order, but direct measurements (made by means of a horizontal microscope) of conidia growing naturally in a culture slide just before their discharge average only very slightly higher. Traces of the torn outer membrane may sometimes be observed as a narrow collar at the base of the papilla. If conditions are favorable, germination may take place at once, and may result in the formation of a mycelium or of a secondary conidium. In the latter case, a germ tube emerges laterally from the conidium, and, after attaining a variable but usually short length, swells at the tip. This swollen tip is cut off as a conidium and discharged in the usual way. The process of germination and formation of a secondary conidium has been followed in water and in prune decoction mounts, and has been found in a typical case to require about 5 hours for its completion (figs. 1–7). If the

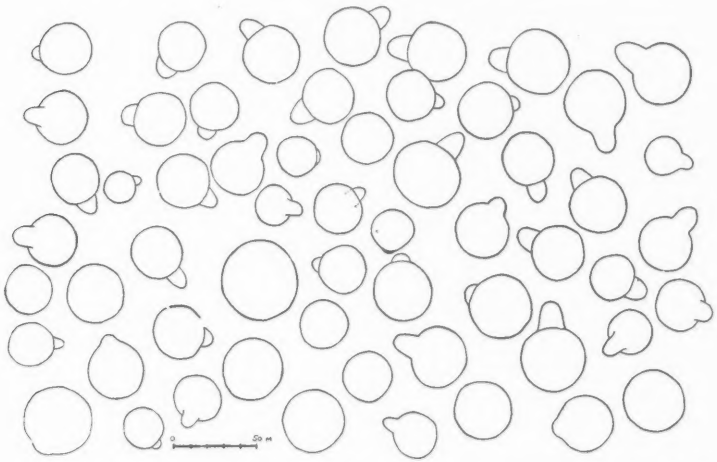

FIG. 3.—Fifty-seven conidia from 42-hour culture on synthetic agar, outlined with camera lucida to show variation in size.

spore is deeply immersed, the germ tube may be very long and more or less branched. In such case the protoplasm is progressively withdrawn from the basal parts of the hypha (fig. 8).

After a culture is a few days old, spores begin to appear which differ from conidia in the possession of numerous cylindrical outgrowths, soft, blunt, and hairlike as a rule; in the thicker wall and darker color of the cell contents, and in the substitituon of an opaque, pluglike structure for the papilla (figs. 12–15). In other respects these spores are exactly like the conidia, and since there may always be found in such cultures a complete series of intermediate stages (fig. 11), the obvious conclusion is that they develop from ordinary conidia and serve as resting spores. A few resting spores have been seen in which the hairs were slightly swollen at the tips. In one culture a very few of the resting spores were provided with distinctly conical, spinelike processes. Intermediate stages were present in all cases, and such aberrant spores seem to represent minor variations due to unknown causes.

In the living fungus the conidia and mycelial parts are filled with a mass of dense, refractive globules. These do not seem to be fatty in nature; at least, they blacken very slowly with osmic acid and do not stain with Sudan III. Because of their presence, no nuclear structures can be seen, either in the conidia or the mycelium. Sections cut 5 μ thick and stained with iron-alum haematoxylin show numerous very small nuclei present. These are spherical or somewhat elongated, and about 1.5 μ in diameter. As is to be expected, they are most numerous in the growing tips of hypae and in the conidia (figs. 20–24). In conidia which have become more or less dormant, the nuclei tend to be distributed near the periphery (fig. 21). The nuclei of the resting cells seem to differ in no respect from those of the conidia (fig. 24). No recognizable division stages of the nuclei have been observed. No traces of conjugation nor of zygospores have been seen.

The occurrence of spores with a roughened or sculptured outer wall is exceptional, but not unknown in the Entomophthoraceae. THAXTER (**6**) describes the zygospores of *Empusa echinospora* as spinose, and SPEARE (**5**) has shown that in *Massospora cicadina* the conidia are verrucose and the resting spores are strikingly reticulate.

BREFELD describes the zygospores of *Conidiobolus utriculosus* as beset with small warts. The resting spores of the species under consideration are quite unlike any of these, however, and in the literature there seems to be no suggestion of the peculiar transformation of conidia into resting spores here described.

The fungus clearly belongs to the genus *Conidiobolus* established by BREFELD to include two species which he found occurring as parasites on species of *Hirneola* and *Exidea*. One species, *C. utriculosus*, is described in detail. BREFELD'S second species, *C. minor*, is based on certain small conidia observed in the cultures of *C. utriculosus*. It was not secured in pure culture, and it seems highly probable that *C. minor* represents small conidia of *C. utriculosus*, reduced in size by repeated germination in exhausted cultures. Similar reduced conidia occur in the case of the species under consideration, when it is growing under such conditions (fig. 25). The species found in Iowa closely resembles *C. utriculosus* in its vegetative and conidial characters. It differs, however, in the size and shape of the conidia, which in *C. utriculosus* are oval and average $35 \times 50\ \mu$ in size, and very markedly in the possession of the curious hairlike appendages on the resting spores. No additional species of *Conidiobolus* seem to have been reported since BREFELD'S original publication. In 1919 GILBERT (3) reported his observations upon a saprophytic Entomophthorous fungus, which he isolated from fern prothallia, without, however, suggesting the genus to which it belonged. There are a number of discrepancies between his observations and those reported in this paper. Thus the primary conidia of the Wisconsin fungus are described as varying from 48 to 60 μ in diameter, as compared with an average of slightly over 32 μ for the form studied in this laboratory. GILBERT found no hyphal bodies; they are abundant in old cultures of the Iowa form. His description of the conidiophores and of the discharge of the conidia is in general agreement with the observations made here when germination takes place under the artificial conditions prevailing in a liquid mount, but does not agree with the observations made upon the Iowa fungus when growing naturally in a slide culture chamber and studied with a horizontal microscope. Under such conditions, the conidiophore is

only very slightly swollen, the inversion of the papilla and the discharge of the conidium are practically simultaneous, the one being the cause of the other, and no portion of the contents of the conidiophore has ever been observed to be discharged with the conidium. GILBERT found old conidia in his cultures becoming yellowish, with a slight thickening of the spore wall, but makes no mention of the curious and striking appendages, nor does he refer to the most striking characteristic of the Iowa form, namely, the regular and gradual transformation of the conidia into the appendaged resting spores. In spite of these discrepancies, it seems probable that the Wisconsin fungus and the one isolated in Iowa represent the same species. While the resting spores are distinctly unusual, there would seem to be little warrant for regarding this character as justifying the establishment of a new genus, when the fungus is clearly related very closely to *Conidiobolus utriculosus* as described by BREFELD. It is therefore described as a new species of the same genus, the specific name assigned to it referring to the villose appendages of the resting spores. The formal diagnosis is as follows:

Conidiobolus villosus, n. sp.—Mycelium abundant, saprophytic, coenocytic, becoming septate and fragmented; hyphae immersed in substratum usually richly branched; aërial hyphae sparingly branched, averaging 12 μ in diameter; conidiophores erect, positively phototropic, not strongly differentiated from mycelium; conidia globose, with large basal papilla, 12 to 46 μ in diameter, averaging 32 μ; conidia on germination give rise either to mycelium or to secondary conidia borne on short conidiophores; under conditions unfavorable for germination, conidia become gradually transformed into resting spores, characterized by thicker walls and darker color, by the contraction of the papilla into a pluglike base, and by the development of numerous soft, blunt, hairlike appendages; germination of resting spores like that of conidia; hyphal bodies abundant in substratum; zygospores unknown.

On *Hypochnus* sp. on sodden, decayed, frondose wood. Iowa City, Iowa, July 1923; also Wisconsin (?).

UNIVERSITY OF IOWA
IOWA CITY

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EXPLANATION OF PLATE XVI

All figures drawn with aid of camera lucida, using Zeiss objective D and ocular 4; reduced about one-third in reproduction.

FIGS. 1–7.—Germination of conidia in prune decoction (figs. 5–7 represent same conidium): fig. 1, conidium from old culture freshly placed in solution; fig. 2, after 2 hours, vacuoles indistinct; fig. 3, germ tube almost complete, 3.5 hours; fig. 4, secondary conidium half formed, 4 hours; fig. 5, old spore almost emptied of protoplasm, 5.5 hours; fig. 6, secondary conidium discharged, conidiophore still turgid, 5 hours, 50 minutes; fig. 7, conidiophore and old conidium wall collapsed, 6 hours.

FIG. 8.—Germinated conidium, 17 hours in prune decoction on slide, showing septate and collapsed tube (over 1500 μ long) with segregated hyphal body, and secondary conidium.

FIGS. 9, 10.—Two conidia with multiple germ tubes, germinated on dry slide in moist chamber.

FIG. 11.—Conidium becoming transformed into resting spore; 15 day culture on agar plate; note fragment of conidiophore wall.

FIG. 12.—Newly formed resting spore, from same culture as fig. 11.

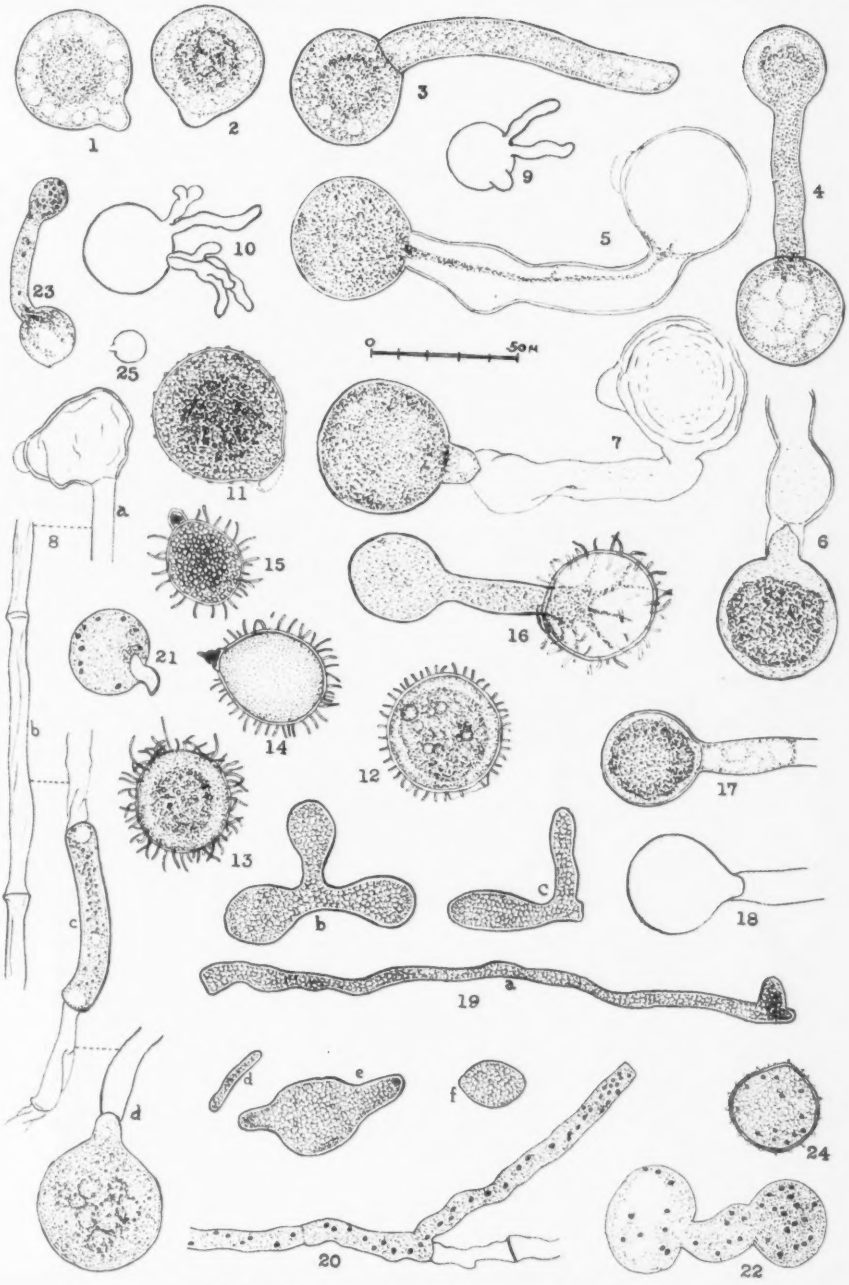
FIGS. 13–15.—Resting spores from surface of 9-weeks' prune decoction culture: fig. 13, hairs more numerous and longer than usual; figs. 14, 15, resting spores shrunken to oval shape, and with papillae transformed into pluglike bodies.

FIGS. 16–18.—Germination of resting spore: fig. 16, secondary conidium nearly formed; fig. 17, conidium ready for discharge, 12 minutes later; fig. 18, conidium discharged, 18 minutes later than fig. 17.

FIG. 19.—*a–f*, Hyphal bodies from 2-months' culture on nutrient agar.

FIGS. 20–24.—Stained sections, to show nuclei: fig. 20, hyphal segment germinating in agar culture, growth toward right; fig. 21, conidium in dormant state; figs. 22, 23, production of secondary conidia; fig. 24, resting spore.

FIG. 25.—Smallest conidium observed, diameter 12 μ.



MARTIN on CONIDIOBOLUS VILLOSUS

POISON CANALS OF CICUTA MACULATA

H. B. SIFTON

(WITH PLATES XVII, XVIII)

The points illustrated in this paper were brought out during a microscopic examination of *Cicuta maculata* L., made with a view to the identification of fragments of the plant in cases of poisoning, and have been thought sufficiently interesting to be worthy of record.

The secretory canals of the Umbelliferae, running in a longitudinal direction in all the vegetative organs, are rather easily observable structures, and their presence has been known for many years. As early as 1866, MÜLLER (4) described the canals in the secondary tissues of the root as schizogenous structures increasing in size with increasing age, but with little or no multiplication of the cells forming their walls. His figures are from *Ferula orientalis*. DEBARY (2) has described minutely their development in the primary cortex.

In the present article, some details observable in the root will first be described. Fig. 1 is from a transverse section of one of the fleshy roots, in which a considerable amount of secondary growth has taken place. The dark line of small cells near the right is the cambium, with the secondary cortex to the left. The tissue produced by the cambium is chiefly parenchyma, and on the cortical side secretory canals are plentiful in this secondary growth. The identity of the cells that are to line the canals is plain at a very early stage, seven cells from the cambium in the youngest canal shown in the photograph. They lie in two rows adjacent to each other, and are to be distinguished by their dark contents. The development of the canal consists largely in the spreading apart of these rows of cells.

One of the young canals in its earliest stage is shown at a higher magnification in fig. 5. The two rows of lining cells are very distinct, almost in contact, but with a narrow slit forming between them at one end. In size they differ considerably from the surrounding parenchyma cells, and it is clear that either the cambium cells which

gave rise to them divided more rapidly than those on either side, or divisions have since taken place in the canal cells themselves. The parenchyma cells in the immediate neighborhood of the canal are gorged with starch. When a root section is treated with iodine, the accumulation of starch around the younger canals is very striking. As the canals increase in size the starch gradually disappears, being used doubtless in the manufacture of the secretion with which the structures are filled. Around the large, fully formed canals starch is no more plentiful than anywhere else in the cortex.

Figs. 6 and 7 show further stages in development of the secretory canal. Fig. 6, taken at a greater distance from the cambium than fig. 5, shows the slit opened out until the canal is lenticular in cross-section. The only additional change is an increase in size in all the cells. This increase is typical of that found throughout the cortex; the outer cells, with the exception of the periderm, are always larger than the younger ones near the cambium. Fig. 7 shows a completed canal such as may be seen to the left of fig. 1. Its cross-section has become more or less circular, and some of the secretion, with which it was originally filled, has been retained through the process of imbedding, cutting, and staining. The lining cells have become much elongated. The drawing away of the protoplasm from the walls of the cells is due to imperfect fixing and imbedding.

Fig. 8 is of a longitudinal section through one side of a canal, and shows the secretory cells in face view. The arrangement of the cells in vertical rows and their shortness in a vertical direction suggest that horizontal divisions have occurred in the process of their formation. This is strengthened by the much greater length of the adjacent parenchyma cells formed by the same cambium. Cells in the process of division, however, have not been found. Outside the area shown in fig. 1 are the canals of the primary cortex as described by DEBARY. A few of them are shown at the right of fig. 2. They resemble closely the fully formed secondary canals just described. When the root is young they are small, but their size increases with age and they also are filled with secretion.

The region of the root inside the cambium contains no canals, a fact of some interest in connection with the varying toxicity of this organ at different seasons of the year. The poisonous principle is

contained in the canals, from which it oozes in the yellowish drops that appear when a fresh root is cut. Much has been written about *Cicuta* from the standpoint of its toxic qualities, and widely differing opinions as to its toxicity have been recorded. It is rather well agreed, however, that the roots are more poisonous in spring and autumn than in summer. JACOBSON (**3**) states:

> Cicutoxin [the poison] is very sensitive to an increase in the temperature above that normal to its formation in the plant, and differences have been observed in the products obtained in April and October from those obtained in July and August. The former is the yellower product and the more toxic, grain for grain, but the midsummer tubers contain the larger quantity of material.

From his experiments it would seem that this is due to polymerization and perhaps partial decomposition at the higher temperature. In addition to this, there is another reason why the bulky roots found in summer are less toxic than might be expected, in that they have a large central region devoid of poison canals. This region is being added to not only by the cambium of the root, but also by divisions and growth in the parenchyma cells of the primary tissues. This growth is illustrated by figs. 2 and 3. Fig. 2 represents a transverse section of the central part of a comparatively small root. The cambium has produced only a small amount of secondary tissue, and the primary wood forms an irregularly star-shaped mass at the center. Fig. 3, from a section of a larger root, shows the primary wood forced apart by the growth and division of the parenchyma cells. The two figures are at the same magnification, but in that of the larger root even the radial rows of cells formed by the cambium on its inner side are beyond the range of the photograph, owing to the extent of the growth of central tissue. In spring none but small roots are to be found, and in autumn the large ones have been reduced to mere withered remnants, all their substance apparently having been used up in the process of seed production. At this time the only fleshy roots to be found are the small ones belonging to the seedlings whose first crop of seeds will not be borne until next year.

To determine whether cicutoxin might be present in the central portion of the root, although canals are absent, the chemical test recommended by TAKAYAMA (**6**) was used, which is quoted by JACOBSON as being efficient in determining the presence either of the

poison itself or of its polymerized and decomposed product. Crushed portions of the root were soaked in a mixture of three parts of phenol to one of ether, and a drop of concentrated sulphuric acid was brought into contact with the solution. This test, when performed on the parts of the root outside the cambium, invariably gave the green color, changing through blue and violet to brown, that is characteristic for cicutoxin and its derivatives, but the result was never obtained when the central part of the root was tested.

The rootstock differs from the root in having a pith, and in the enormous size attained by the secretory canals. Fig. 4 is from the cortical portion of the rootstock, and is at the same magnification as figs. 1–3. The right of the photograph is toward the cambium. The large canals with distorted and torn parenchyma between them are prominent in the figure, and a few smaller ones are to be seen nearer the cambium. The pith also contains canals, but these have not been illustrated. Like those of the cortex, they grow to a size unequaled either in the root or in the aerial portions of the plant.

The stem proper has no canals in its secondary tissues. In its cortex a single primary canal is opposite each of the larger fibrovascular bundles. These canals do not grow with the increasing size of the stem, but on the contrary often appear flattened as if crushed by the growing tissues. Fig. 9 shows one of the fibrovascular bundles of a stem where a great deal of secondary growth has taken place. Opposite the crown of primary bast, and separated from it by two layers of cortical parenchyma, is one of the small, flattened canals whose lumen is almost eliminated, although the dark walled lining cells are quite clear.

Like the rootstock, the aerial stem has canals in its pith. In a stem the size of that from which fig. 9 was made, the pith is hollow except at the nodes, owing to the breaking down of its central cells. Imbedded in the remaining peripheral tissue are a few small canals. Although there is an abundance of room for growth, owing to the breaking down of most of the medullary tissue, these canals do not enlarge, but remain like those of the stem cortex in size. They, however, do not attain the flattened appearance that has been described for the latter.

Accompanying the vascular bundles through the petioles to the leaves are small canals similar to those in the stem, with which they probably connect, although a determination of this connection was not made. The large ducts in the fruits are too well known to require more than a passing mention.

It should be noted that the scarcity and small size of canals in the stem and leaves, as compared with those of the root and root-stock, correspond with the comparative lack of toxicity of the former organs. Numerous deaths from poisoning by the underground parts of the plant are on record, the action being very rapid, even in cases where cooking may be held to have destroyed a great deal of the cicutoxin originally present. Moreover, the amount necessary to produce death is very small. On the contrary, cases of death from the stems and leaves are very rare. PAMMEL (5) states a case where some cattle and a horse were made ill, but not killed by eating leaves of the plant in hay. JACOBSON quotes from CAILLARD (1) the case of a man who obtained and ate large quantities of the young stems and leaves of *Cicuta virosa* in an attempt at suicide. Although very ill, he responded to treatment and recovered. JACOBSON states:

> Experiments both in this laboratory and elsewhere have brought out the fact that the dried stems and leaves of the *Cicuta occidentalis* class have not been found to be poisonous except in the early spring, and then the cicutoxin is present only in minute quantities.

The explanation of this is made clear by the anatomical study of the plants.

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DESCRIPTION OF PLATES XVII, XVIII

PLATE XVII

FIG. 1.—Transverse of mature fleshy root; cambium at right, with secondary cortex to left; ×48.

FIG. 2.—Transverse of central portion of young root; ×48.

FIG. 3.—Transverse of central portion of larger root; ×48.

PLATE XVIII

In all figures of this plate, right of photograph is toward central axis of plant.

FIG. 4.—Transverse of rootstock; many large canals; ×48.

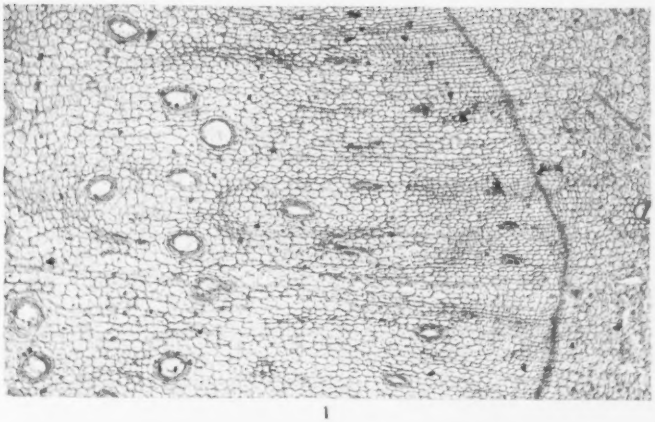
FIG. 5.—Transverse of secondary cortex of root near cambium; canal just beginning to open; ×307.

FIG. 6.—Transverse of same farther out from cambium; canal midway in its development; ×307.

FIG. 7.—Transverse of same still farther from cambium; completely formed secondary canal; ×307.

FIG. 8.—Radial of same; wall of canal in face view; ×307.

FIG. 9.—Transverse of stem; bast and secondary wood of one fibrovascular bundle; collapsed primary cortical canal to left of crown of phloem; ×103.



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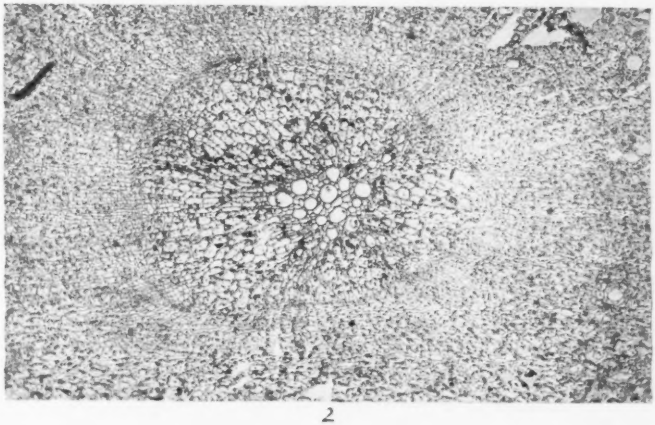

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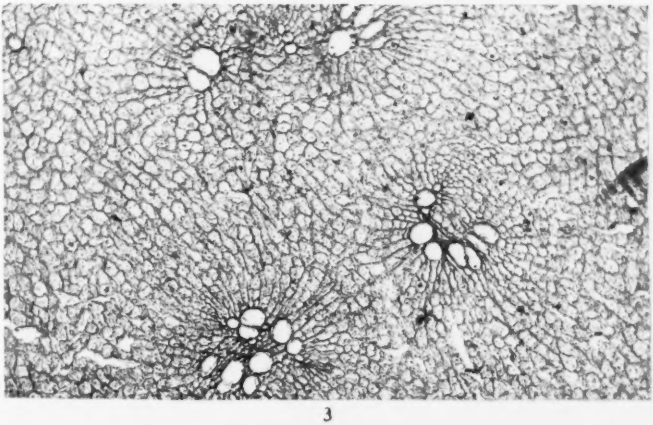

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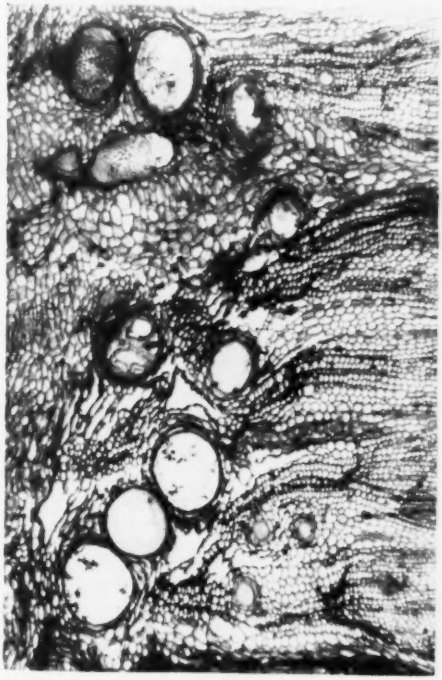
SIFTON on CICUTA MACULATA



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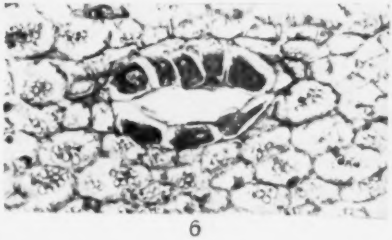

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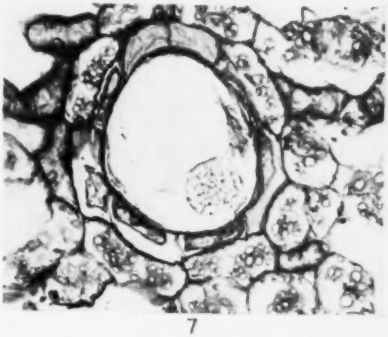

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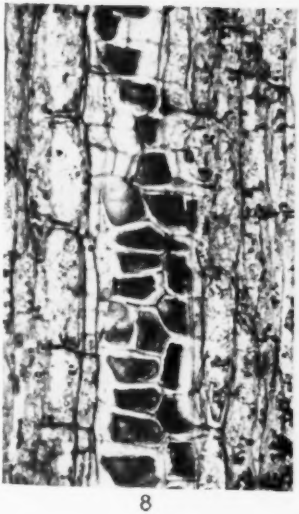

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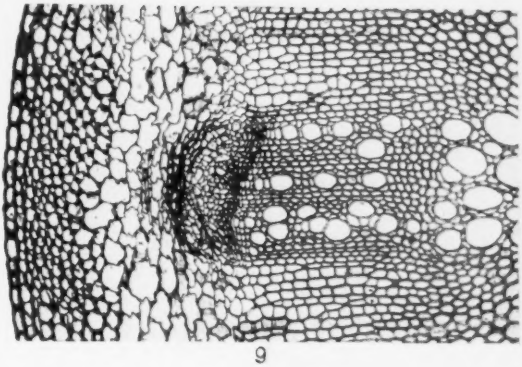

9

SIFTON on CICUTA MACULATA

THE PECTINASE OF SCLEROTINIA CINEREA

GEORGE W. MUHLEMAN

Introduction

Sclerotinia cinerea attacks certain species of non-resistant plums. It is commonly called the brown rot fungus because of the color which seems to develop after the fungus has attained a certain growth. The infected plum turns brown, but is quite solid, even when well rotted. The term *Sclerotinia*, therefore, indicates sclerosis or hardening, and *cinerea* refers to its cinder-like appearance. The writer has observed that when the fungus has been allowed to grow three or four days on prune juice it has a grey color, and so remains until the mycelium has been ground up, when the oxidases cause it to turn to colors ranging from a very light to a dark chocolate color.

When the mycelium is observed under the microscope, it is found to be segmented in appearance, similar to *Spirogyra*. The spores are greatly branched, and have the appearance of the yeast plant after it has budded and branched.

The spores when formed in great profusion have a rust colored appearance, and seem to arrange themselves in a series of circular areas. The right conditions for the formation of spores has been one of the quests of this investigation, and will receive further attention as this investigation proceeds. The fungus seems to be rather erratic; sometimes the spores are best formed in the dark and again they are best formed in the sunlight. This investigation, however, has demonstrated that a nutrient medium can be inoculated either with the spore or by introducing a filament of the mycelium, a convenience if one has not always on hand a supply of spores for inoculating purposes. Nevertheless, the method of inoculating by dusting in the spores is by far the more satisfactory, because of the uniformity with which the spores become distributed over the surface. Usually from thirty inoculations the growth was quite uniform, except in the case of possibly three or four flasks.

The fungus was grown in an incubator cooled by passing tap water through the jacket, and also by placing the Erlenmeyer

flasks containing the cultures on top of the laboratory table and in the trough of the table. Some of the flasks were covered and some were not. The room temperature was 26° C. The control conditions of light and temperature seemed to make no appreciable difference in the growth of the fungus or in the production of spores, hence the flasks containing the nutrient prune juice after inoculation were simply placed on top of the laboratory table. Sporulation of *Sclerotinia cinerea* grown on prune juice occurred at from 5 to 13 days, and in other cases spores never formed. Peaches that had been soaked in distilled water for 24 or 48 hours, and then autoclaved and inoculated, in some cases produced abundant spores in 3 days, while some peaches inoculated at the same time never produced spores. If, instead of soaking the peaches 24 hours before autoclaving and inoculating, one simply placed dry peaches in Petri dishes containing distilled water, and placed them in the autoclave until the peaches had softened, these could not be inoculated at all, presumably because the peaches had been bleached with SO_2, and the presence of the SO_3 or SO_4 radical inhibited all fungus growth.

After growing a crop on prune juice, attempts to grow a second crop on the same juice resulted in a much slower growth, as well as a smaller yield. The color of the prune juice was made very dark as a result of one growth. There did not seem to be a very great decrease in the volume of the prune juice after the growth of the fungus. These observations are to be continued.

The peaches when placed in Petri dishes and sterilized became infected by one of the black fungi if allowed to stand for a period.

An attempt was made to grow *Sclerotinia cinerea* on a peach that had been soaked and then mashed out flat on the bottom of the Petri dish and sterilized. No growth was possible. An attempt to grow this fungus on nutrient agar spread out on the bottom of the Petri dish was also only partially successful.

The specimens used in this study were secured from the plant pathology laboratory of the University of Minnesota, from a "mummy" found under a plum tree in the plum orchard of the Farm School of the University, and from an infected plum found in a plum orchard near Mora, Minnesota.

The best sporulation was secured when the fungus was grown on peaches. Prune juice was used for the growth of the felts from which the pectinase was secured.

The method of preparing the peaches and the prune juice was to place the dry peaches and dry prunes in distilled water, and keep in the icebox 24–48 hours. At the end of this time both the peaches and the prunes were nicely swollen and soft. The prunes used were a large meaty variety. The peaches were removed from the liquor, and one or two halves were placed in a Petri dish and autoclaved for 30 minutes at a pressure of 15 pounds. After they were cooled they were inoculated from the spores by dipping a coil of sterile wire on to the spores, and then dusting them on to the peaches. Perceptible growth of the spores took place at room temperature in from 2 to 3 days, and at the end of 5 days in most cases sporulation had occurred.

The prune juice was prepared by placing the large beaker, in which the prunes had been allowed to soak, in the autoclave and cooking 20–30 minutes at 15 pounds pressure. The entire contents were then poured into the basket of a hand press lined with a heavy cloth, and subjected to pressure. The pits were then removed from the prune pulp and the pulp placed in more distilled water and again autoclaved. This process of expressing the juice and cooking the pulp in the autoclave was continued only so long as a juice of specific gravity 1.03 was secured. The juice thus secured was thoroughly mixed, and the specific gravity determined and marked on the outside of the flask. About 250 cc. was placed in Erlenmeyer flasks which were stoppered with cotton, and the contents autoclaved for 15 minutes at 15 pounds pressure. As juice was needed from time to time, it was taken from these flasks and either diluted to the specific gravity desired or used as it was prepared.

There was placed in a series of 300 cc. Erlenmeyer flasks 20 cc. of prune juice, a volume sufficient to cover the bottom of the flask; the flasks were stoppered with plugs of cotton, and autoclaved for 15 minutes at 15 pounds pressure. In the first attempts at inoculating, the sterilized loop of wire, after touching the spores, was dipped beneath the surface of the prune juice. No growth of the fungus resulted from this method of inoculating. In every case when the

wire laden with spores was tapped on the lip of the flask, the spores thus dusted on to the prune juice grew in great abundance.

To prepare an active pectinase solution, three different methods of procedure were employed. (1) The method outlined by BROWN.[1] After the mycelium had grown sufficiently, the felts were removed from the flasks, washed in water to remove all the liquor, and then washed twice in acetone. These washed felts were then exposed to the air to allow the acetone to spontaneously evaporate, and afterward dried in a desiccator charged with fresh quicklime. This dry mycelium was then ground with an equal weight of silica and mixed with water in the ratio of 0.2 gm. of the ground substance to 3 cc. of distilled water. (2) The felts were removed from the prune juice in which they had grown, washed in running water until free from prune juice, dried between cloths, thoroughly ground in a mortar with silica, and placed in a hydraulic press and subjected to a pressure of 400 kg. per sq. cm. for 30 minutes. The juice thus secured showed a marked activity. (3) The felts were removed from the culture media, thoroughly washed in running water, dried between cloths, ground up in a mortar with silica, and then triturated with enough water to make a mixture of the same limpidity as that prepared under the first method.

By repeated experimentation it was found that the average weight of the dry felts grown on 20 cc. of prune juice in 5 days was about 0.18 gm.; therefore to determine the weight of silica to be added to the wet felts, the number of flasks was multiplied by 0.18. The last method of preparing a macerating solution was the simplest, and the one involving the least expenditure of energy. The task which is to engage my attention later is to prepare a solution that will be standard in its concentration of enzymes.

HARTER and WEIMER reported that, in their work with certain species of *Rhizopus*, they secured an active pectinase solution by using the media in which they grew their fungus. In no case has the writer been able to secure any evidence of the pectinase enzyme in the prune juice media after growing a crop of *Sclerotinia cinerea*. The evidence of maceration was tested out on green plums, green

[1] BROWN, W., Studies in the physiology of parasitism. Ann. Botany **29**:313–348. 1915.

apples, green peaches, and ripe potatoes cut in sections 0.5 mm. thick. An attempt was made also to precipitate the enzyme from solution by using ethyl alcohol and purifying in the usual way. Here again negative results were secured.

With an active pectinase preparation, the disks were macerated 1.5–4 hours. These disks were sectioned with an ordinary microtome set to cut 0.5 mm. thick. The apple and plum disks were reduced to a sauce and the potatoes to a fine pulp. The disks when cut, even after remaining in water for a number of days, were very resistant to being pulled apart, but after maceration they were very easily separated by lightly holding between the thumb and forefinger. This was the usual method for testing maceration.

The pectinase solution was preserved in toluene, and the maceration was carried on with toluene added as a preservative, the amount added being just sufficient to give to the mixture a strong odor of the preservative. Later studies may require a resort to quantitative methods of procedure. The macerating solutions thus preserved have retained their activity from one week to three months. When a standard solution has been prepared, perhaps there will be no variation as to the time the solution remains active. It was found that 10 or 12 felts would provide material to prepare the necessary macerating media. In grinding the mycelia one always stopped when the pulverized mass no longer adhered to the pestle or to the mortar. An attempt to use a meat grinder to hasten the work of grinding was found impracticable, as the material clung to the chopper and clogged it.

After it was determined that *Sclerotinia cinerea* of 3, 4, or 5 days' growth gave the most active pectinase solution, it was further discovered that it could be ground up in a mortar in a few minutes. The color of the felts and the color of the ground material, and not exactly the age of the crop in days or hours, must govern one's conclusion as to its activity. In every case of the score or more active preparations made, the color of the ground mass was a light chocolate. The longer the fungus was allowed to grow the tougher and thicker became the felt. Attempts to secure an active pectinase solution from old growths were failures.

To determine whether the specific gravity of the prune juice

has any influence on the rapidity of the growth of *Sclerotinia cinerea*, duplicates of three flasks were inoculated with the following concentrations of prune juice: specific gravity 1.04, 1.05, 1.06, 1.07, 1.08, 1.09, 1.10, 1.11. These were all inoculated from spores grown on autoclaved peaches. There did not seem to be any perceptible difference as to the amount of growth. The relative macerating activity of the enzyme from these different cultures will be taken up in later experimentation. The heaviest spore growth seemed to have taken place on felts grown on prune juice with specific gravity 1.04, and this was the concentration employed in further studies.

Summary

1. Spore formation and methods of inoculating with spores and with mycelium are discussed.

2. Methods of growing the fungus on different media are described.

3. One growth of fungus seems to unfit prune juice for growing further crops.

4. Methods of preparing culture media which give maximum growth are described.

5. Three different methods of preparing an active pectinase solution are compared.

6. *Sclerotinia cinerea* does not excrete pectinase into the culture media.

7. The disks used in testing maceration were 0.5 mm. thick, and were from apples, plums, peaches, and potatoes. The tensile strength was determined with the fingers.

8. It has been demonstrated that the color of the felts of *Sclerotinia cinerea* is a good index of the activity of the pectinase solution which may be prepared.

9. The specific gravity of prune juice has been studied.

HAMLINE UNIVERSITY
ST. PAUL, MINN.

POLYEMBRYONY IN CERTAIN POLYPODIACEAE AND OSMUNDACEAE

DAVID M. MOTTIER

(WITH THREE FIGURES)

During the years 1920 and 1921, a graduate student in the botanical laboratories of Indiana University carried out some experiments in the development of several embryos on single gametophytes of certain species of Polypodiaceae, the results of which have been published elsewhere.[1] ETTER's experiments, which were necessarily brought abruptly to a close, not only gave promise of further positive results, but suggested also other lines of study. The writer, therefore, continued the study of the experimental development of polyembryony, and at the same time began a series of investigations of a similar character which are still in progress. In ETTER'S paper will be found a résumé of the more important literature available.

Method

Stock cultures of the prothallia were first made, and, as soon as the plants had attained a width of 2–4 mm. across the wings, thrifty individuals were carefully transplanted to separate dishes and kept under the best cultural conditions available. Fig. 1 illustrates the method of cultivation. All cultures were made upon sterilized woods earth, in ordinary flower pot saucers, which were covered with bell-jars. The cultures were watered by sub-irrigation and never by sprinkling or spraying. In case the plants touched one another, or in any way became crowded because of increase in size, a number of the specimens were again transplanted to other dishes.

As soon as the prothallia had attained a diameter of 10–15 mm., fertilization was accomplished by hand. The time required for the attainment of this size varies with the season, the plants growing more rapidly during the spring and summer months. The record of the plants shown in fig. 1 is as follows: spores sown October 11,

[1] ETTER, AUSTIN, Polyembryony developed under experimental conditions in certain polypodiaceous ferns. Bull. Torr. Bot. Club **50**:95–107. 1923.

transplanted December 30, 1922, and photographed (natural size) February 28, 1923. These plants, therefore, were nearly four months old. Needless to say, it was necessary to prevent fertilization during this period by care in sub-irrigation, and by preventing the falling of drops of water upon the plants.

FIG. 1.—Four months' old prothallia of *Matteuccia nodulosa* (Michx.) Fernald, grown upon woods earth in flower pot saucer, showing method of cultivation; natural size.

To accomplish fecundation, a few drops of water were placed upon the prothallia near the growing point. The best time was found to be near midday during sunny weather. In prothallia that tend to be dioecious, like those of *Matteuccia nodulosa* (Michx.) Fernald, a small tuft of male prothallia was placed near the apical sinus before the water was applied.

Observations

In these studies the following species supplied the material: *Matteuccia nodulosa* (Michx.) Fernald, *Dryopteris mollis* (Jacq.) Hieron., of the Polyopdiaceae; and *Osmunda Claytoniana* L., of the Osmundaceae. *Pteris longifolia* L. is also a suitable plant because of the ease with which prothallia can be grown.

The process of fertilization was repeated two or more times on as many successive days. One of the objects was to determine how many self-sustaining sporophytes could be produced on a single prothallium before the latter began branching by offshoots or proliferations. In *Dryopteris*, *Matteuccia*, and *Osmunda*, as many as five sporophytes could be brought to the stage of independent growth on a single prothallium before the latter began to show signs of exhaustion, which was indicated by the cessation of growth and gradual exhaustion. Three or four sporophytes, drawing at least a part of their nourishment from the parent gametophyte, soon accomplished the exhaustion of the latter. In addition to the large, self-nourishing sporophytes, one or more embryos of microscopic size were sometimes detected. If, however, the first sporophytes were carefully amputated, a larger number could be produced. With some care, and after a little practice, a steady hand can amputate, or remove by plucking away, a sporophyte that has its first leaf and root large enough to be seized with the forceps. The amputation is made flush with the under surface of the prothallium. A very sharp lance-pointed needle, a "razornife," or a safety razor blade provided with a handle is a suitable tool.

After the prothallia have attained a certain size and age they begin to develop branches or proliferations. This behavior was especially pronounced in certain specimens of *Dryopteris mollis*. The proliferations, generally heart-shaped, usually arise from the under surface on either side of the archegonial cushion, now developed into a distinct midrib. Proliferations may also spring from the margins of the wings, and from both anterior and posterior portions. Even after the older portion of the midrib has become brown on the surface, proliferations will spring from the tissue beneath. The proliferations may be numerous, and each may develop a sporophyte

after fecundation. Fig. 2 shows a prothallium of *Dryopteris mollis* with eleven heart-shaped proliferations, ten of which bear a rooted sporophyte. These proliferations are all a part of the parent prothallium, and the whole constitutes one branched gametophyte. In the beginning of this experiment one sporophyte and also by acci-

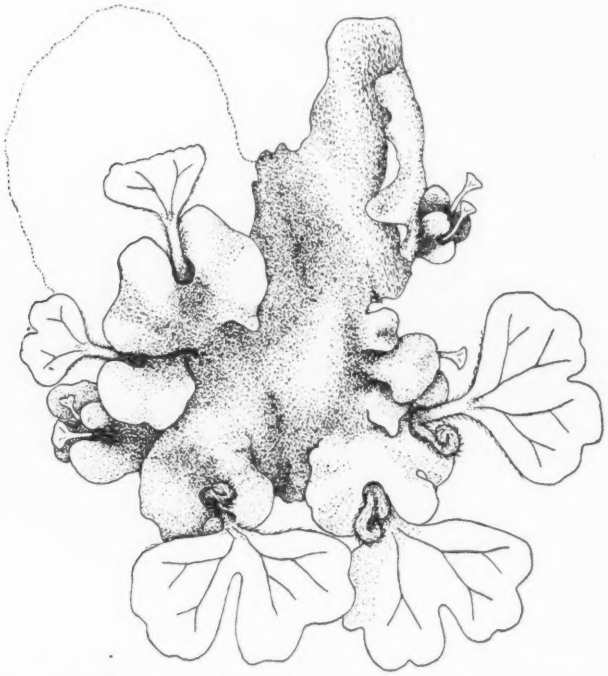

FIG. 2.—Enlarged drawing from photograph of prothallium of *Dryopteris mollis*, showing eleven marginal proliferations, ten of which bear one rooted sporophyte each; ×5.

dent the left wing of the gametophyte were cut away. The amputated wing is indicated by the dotted line.

Fig. 3 illustrates another interesting result in *Dryopteris mollis*. Before proliferations began to develop on this prothallium, two sporophytes were successively amputated at different times. In the process of amputation the two lobes or wings of the prothallium were slightly injured. They stood up almost at right angles to the midrib,

and soon withered, doubtless as a result of injury in handling. Before the outline drawing of this figure was made, the injured lobes were carefully cut away so that the proliferations might plainly be seen. These proliferations, which were mostly heart-shaped, numbered seventeen. They sprang from both sides and from the ends of the midrib, as shown in the figure.

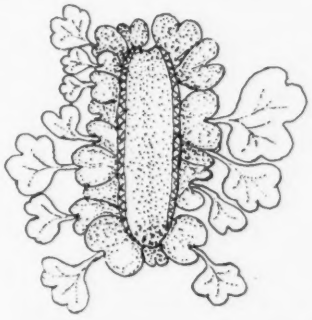

FIG. 3.—Diagrammatic drawing of prothallium of *Dryopteris mollis*, from which the first two sporophytes were amputated; subsequently the 13 or 14 proliferations developed from the sides of the midrib on the under side; eleven of these had borne as many sporophytes, making 13 in all; ×5.

Of these seventeen proliferations, eleven had produced a rooted sporophyte at the time of harvesting the specimen for critical observation. These lobes are all too small to produce such vigorous sporophytes unless attached to a parent plant. Each lobe or proliferation, whether heart-shaped or not, bore both antheridia and archegonia.

In cultures of *Dryopteris mollis* extending over two years, in which the plants were grown upon earth under the most varied conditions, not a suggestion of real apogamy was ever observed. That we are dealing with a single, although much branched gametophyte there can be no doubt, inasmuch as the proliferations or branches form one continuous tissue complex. The prothallia of figs. 2 and 3 are truly as individual as two maple trees.

Few plants outside the liverworts lend themselves more readily to experimentation than certain fern prothallia, especially when phenomena of regeneration are sought. Any part of the prothallium, if carefully severed at the proper time, and suitably cultivated, will regenerate a new individual.

The writer has not carried experimentation in the production of plural sporophytes on a single gametophyte further than the cases cited in the foregoing, for other phenomena came under observation in the series of experiments which seemed to offer interesting and important results. One of these was the behavior of the pro-

thallia under prolonged cultivation, in which the plants were not permitted to bear sporophytes. A brief preliminary report of methods and results was made before the Botanical Society of America at the Cincinnati meeting of 1923. The cultures continue to reveal such interesting and definite results, that publication of a more complete report will be deferred to a later date.

Summary

1. Under experimental conditions individual prothallia of *Dryopteris mollis* (Jaq.) Hieron., *Matteuccia nodulosa* (Michx.) Fernald, together with certain other polypodiaceous species, and *Osmunda Claytoniana* L. may be made to produce from two to many sporophytes.

2. If the prothallia are permitted to attain a size of 1–1.5 cm. in width across the wings before fecundation is effected, as high as five independent and self-nourishing sporophytes may be developed before the weakening or partial exhaustion of the gametophytes.

3. If the sporophytes are carefully amputated as soon as they become plainly visible, a succession of sporophytes can be produced on an individual prothallium.

4. If the massive prothallia develop proliferations as a result of the experimental cultivation, from ten to fifteen or more sporophytes may be produced.

INDIANA UNIVERSITY
BLOOMINGTON, IND.

BRIEFER ARTICLES

AN ABNORMAL ARCHEGONIUM OF FUNARIA HYGROMETRICA[1]

(WITH ONE FIGURE)

In 1908 the writer[2] called attention to an abnormal archegonium found in *Porella*, and referred to the literature bearing on somewhat similar cases in other plants. The archegonium shown in fig. 1 was found in *Funaria hygrometrica* which had been grown in a greenhouse. The spores had been sown on sterilized soil, and they produced in the usual way a great number of plants which were densely crowded together. It will be seen that the archegonium differs from the usual type in having two egg cells, and, in addition to the usual single chain of canal cells, part of a second row of two canal cells and a ventral canal cell. The two egg cells are rather large. The archegonium itself was somewhat larger than the others observed. The figure was drawn with a camera lucida after having been cleared in glycerine, as in my drawing of *Porella*.

The position of the egg cells, ventral canal cells, and canal cells were placed side by side as shown in my figure of the archegonium of *Funaria hygrometrica*. These cells are placed in a row above one another in alternating positions, as shown by COKER[3] for *Mnium* and by BLISS[4] for *Polytrichum juniperum*.—F. M. ANDREWS, *Indiana University, Bloomington, Ind.*

[1] Since the preparation of this article, a similar case has been found by EMIG (Twin eggs in *Bryum caespiticium*. The Bryologist 1924: p. 94).

[2] ANDREWS, F. M., An abnormal *Porella platyphylla*. BOT. GAZ. **45**:340. 1908.

[3] COKER, W. C., On the occurrence of two egg cells in the archegonium of *Mnium*. BOT. GAZ. **35**:136. 1903.

[4] BLISS, MARY C., On the occurrence of two venters in the archegonium of *Polytrichum juniperum*. BOT. GAZ. **36**:141. 1903.

FIFTIETH ANNIVERSARY ISSUE

The first number of the BOTANICAL GAZETTE, then known as the *Botanical Bulletin*, was issued at Hanover, Indiana, in November, 1875. With this issue, therefore, the Gazette reaches the golden anniversary of its founding. It is an appropriate time to look back over the half century of progress made since the Gazette began its career of service to botanical science.

During the early years of publication, four to eight or twelve pages a month sufficed to carry the material sent in for publication, and the editor repeatedly urged botanists to send in notes of interest and value. The notes were usually very brief, a paragraph or two, seldom a page in length, and were mainly taxonomic, and geographic, interesting observations on plant distribution, unusual locations, local lists of species, or comments on recent discoveries. Botany then was still dominated by the naturalistic phases of the subject.

Publication in those days was relatively inexpensive. Although the subscription price of the BOTANICAL GAZETTE in the beginning was only $1.00 per year, and the subscription list about 100, the deficits were not large, and after the first two years the Gazette paid its own way, even without advertising matter, which was not admitted until the beginning of the fourth volume, in 1879.

The BOTANICAL GAZETTE has made a wide appeal to botanists from the very beginning. During the first ten or fifteen years after its founding, it carried the names of a large array of noted botanists appended to the published notes. ASA GRAY, whose interest was warm and personal from the start, contributed frequently to its pages, and ENGELMANN, BESSEY, VASEY, EATON, BEAL, CHAPMAN, PECK, HOOKER, SARGENT, RUSBY, BARNES, and many others made it their medium of communication with their fellow botanists.

The growth of the BOTANICAL GAZETTE during the last forty years reflects the enormous advances made by the science of botany during this period. Morphology led the advance out of the naturalistic period, with great contributions to our knowledge of the phylogeny of the great orders of plants. A little later plant physiology and ecology shared in the rapid development of our knowledge of plant life, and the Gazette has carried in its pages many of the most important discoveries made during the last quarter of a century.

Although the BOTANICAL GAZETTE began its career at Hanover, Indiana, it has gone with its editor from place to place in his career as investigator and teacher. From Hanover it went to Crawfordsville in

1879, to Bloomington in 1891, to Lake Forest in 1893, and finally to Chicago in 1896. The printing has been done by the University of Chicago Press for almost thirty years, and a very high standard of excellence in form and workmanship has been established.

As the Gazette begins its second half century of service to botanical science, the progress made during its career thus far gives us hope and courage for the tasks of today and tomorrow. Although Professor JOHN M. COULTER, founder and able editor of the Gazette ever since its founding, is retiring from active service at the University of Chicago, he retains the editorship of the journal, and the BOTANICAL GAZETTE looks forward to an ever increasing service to botanical science, and through it, to human welfare.—C. A. SHULL, *University of Chicago.*

CURRENT LITERATURE

BOOK REVIEWS

Biology of the flowering plants

A book of more than usual interest and value to the general student of botany has been written by SKENE,[1] who bases his discussion of the higher plants on the firm foundation of experimental physiology. He has summarized the results of a large amount of the modern research upon plant life and plant behavior, and presents a wealth of detailed information, but does it so skilfully that the general picture of plant life is not distorted or obscured by the mass of details. It seems to the reviewer to be a very well balanced discussion, and is written in a style that holds the interest closely. It will be especially helpful to students who desire to keep a broad grasp of the facts while specializing in some particular field of botany.

There are only six chapters, but each covers a very broad field in the life of the plant. The first deals with the fundamental soil relationships, root systems, and the absorption of water and salts. This is followed by a long chapter on assimilation of carbon, and transpiration, which repays careful reading. Chapter iii considers special modes of nutrition, parasitic, saprophytic, mycotrophic, and symbiotic nutrition, and insectivorous plants. The last three chapters discuss mechanical problems and protection; reproduction and dispersal; and development.

The bibliography at the close of the work contains about 600 citations, and one finds among them most of the outstanding contributions in recent years. The American literature has been used freely, and good judgment is shown in the selection and presentation of the material. The fair minded critical spirit of the author is very commendable. All students who desire a well rounded view of the plant as a living organism should have it upon the convenient book shelf.—C. A. SHULL.

Oecology of plants

The appearance of a second English edition of WARMING's book on plant ecology[2] will indicate to a certain extent the importance of his contribution to this branch of science, and its growth since the first edition appeared in 1909. It is gratifying to recall that Professor WARMING lived to see the development of strong ecological schools in England and America, as well as in his native

[1] SKENE, MACGREGOR, The biology of the flowering plants. 8vo. xii+523. New York: Macmillan Co. 1924.

[2] WARMING, EUG., Oecology of plants. An introduction to the study of plant communities. 2d ed. Eng. transl. by GROOM and BALFOUR. 8vo. pp. xi+422. London: Oxford Univ. Press. 1925. $5.00.

Denmark, resulting from the stimulating influence of his "Plantesamfund" that appeared thirty years ago. This reprinting of the English edition of his great work is a fitting tribute to his memory.—GEO. D. FULLER.

MINOR NOTICES

A simple guide to trees.—CURTIS[3] has prepared a neat little book on trees, primarily for the use of boy scouts and campfire girls, but which will be useful for all who wish to readily identify our common trees without the usual technicalities and difficulties of the ordinary manuals. There is an illustration for almost every species presented, and the keys to genera and species are simplicity itself. The author has certainly succeeded in what he undertook to do.—H. C. COWLES.

NOTES FOR STUDENTS

Tertiary plants from western states.—A series of papers has recently been published by CHANEY, dealing with the distribution of certain Tertiary floras from western United States, and with their relation to groups of living plants now found in the same general regions. CHANEY's investigations are not only interesting from the points of view of floral distribution and geological history, but he also draws important conclusions upon the ecological features as shown by these Tertiary floras.

The first paper[4] deals with the similarity between the Bridge Creek flora found in the Tertiary of the John Day Basin and other parts of Oregon, and the living redwood forest of the Coast Ranges of California. He discusses the principles governing the determination of fossil plants, and his own method in particular. He calls it the "ecological method," and the procedure is as follows. He first compares the fossil flora with a list of eligible genera at present found in the region where the fossils were deposited. When possibilities for matching these have been exhausted, the genera of the surrounding regions are considered, and then the genera of the continent. This method differs considerably from that pursued by the paleobotanists of the older schools like HEER, ETTINGSHAUSEN, LESQUEREUX, who did not hesitate to connect the fossil plants of their localities with the species and genera found in tropical and distant regions. This fact may account for the great mixtures of floral elements which those men claimed to have observed in the Tertiary.

After a careful study of the composition of the Bridge Creek flora, CHANEY discusses the climatic and topographic indications, and their geologic correlation. He concludes that the Bridge Creek flora is found in Oregon in beds of probable Oligocene age, and that a similar group of plant fossils is scattered widely in the Tertiary of the Northern Hemisphere. It has a most conspicuous

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[3] CURTIS, C. C., A guide to the trees. 8vo. pp. 208. *figs. 207*. New York: Greenberg, Publisher, Inc. 1925.

[4] CHANEY, R. W., A comparative study of the Bridge Creek flora and the modern redwood forest. Carnegie Inst. Washington, Publ. no. 349. pp. 22. 1925.

element formed by a group of species whose modern relatives are now represented in the redwood forest flora, and because of this relation the physical conditions under which the Bridge Creek forest lived were probably similar to that of the present day redwood forests of the Coast Ranges of California. The climate appears to have been temperate and moist. The shales containing the Bridge Creek fossils are made up largely of volcanic material which was blown and washed into basins of deposition in forested valleys.

The second paper[5] deals with the Mascall flora located on the Van Horn ranch near Dayville, Oregon, on the east fork of the John Day River. The same method is applied here as in the paper previously discussed. The Mascall flora is common in the Great Basin portions of Washington, Oregon, Idaho, Nevada, and California, but occurs also in west-central California, where its composition is less typical than in the Great Basin. It had been described by KNOWLTON[6] more than twenty years ago, and fine collections of the Mascall flora are found in the New York Botanical Garden, the American Museum of Natural History, and Princeton University. CHANEY concludes that the Mascall flora belonged to the Middle or Upper Miocene, and that it represents a climax forest formation which would indicate a lower relief and a climatic condition similar to the one at present in this same region.

The third paper[7] deals with a new fossil leaf species from the John Day series of Oregon, and with a description of a fruit species from the Fork Rivers formation of South Dakota. The author offers the following explanation for differences in character of the *Celtis* record in the Bridge Creek shales and in the White River clays. The Bridge Creek shales were laid down in a moist region, as indicated by the character of the flora as a whole, and the hackberry trees appear to have occupied the forest borders and the slopes at some distance from the water bodies. The White River clays were laid down in an arid or semi-arid region, as indicated by the almost complete absence of fossil leaves, and the hackberry trees occupied the immediate borders of the intermittent water bodies. CHANEY suggests, on the basis of the fossil and living hackberries, that climatic changes and the resultant vegetational development in South Dakota and Oregon have been somewhat similar from the Tertiary up to the present time, but that in Oregon they have been lagging behind the changes in South Dakota.

CHANEY's fourth paper[8] deals with *Umbellularia*, a genus of the laurel family, which is now limited to western California and southwestern Oregon,

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[5] CHANEY, R. W., The Mascall flora, its distribution and climatic relation. Carnegie Inst. Washington, Publ. no. 349. 23–48. 1925.

[6] KNOWLTON, F. H., U.S. Geol. Surv. Bull. 204. 1902.

[7] CHANEY, R. W., Notes on two fossil hackberries from the Tertiary of the Western United States. Carnegie Inst. Washington, Publ. no. 349. 49–56. 1925.

[8] CHANEY, R. W., A record of the presence of *Umbellularia* in the Tertiary of the western United States. Carnegie Inst. Washington, Publ. no. 349. 57–62. 1925.

reaching its greatest abundance and largest size in the former state. In connection with his studies of the John Day and other Tertiary floras in the west, the author has collected a considerable number of leaf specimens that appear to be referable to this genus. He has counted over twenty thousand fossil specimens at the Bridge Creek locality, and found that the recent *U. integrifolia* made up 8.82 per cent, which indicated to him that its representation in the Oligocene redwood forest was on the same order as that of the living species in the related forests of western California. This species, which resembles so closely the recent *U. integrifolia*, was named *Fraxinus integrifolia* by NEWBERRY in 1882. It is called by CHANEY *U. oregonensis*, since generically it is indistinguishable from the living California laurel *U. californica*.—A. C. NOÉ.

Mycorrhiza in the Ericaceae.—Continuing her researches on *Calluna vulgaris*, Miss RAYNER[9] is unable to confirm the results of CHRISTOPH,[10] who claimed that he had produced vigorous seedlings on sterilized soil with roots entirely free from any fungal infection. All seedlings from unsterilized seed seem liable to infection from fungi in the seed coats, in spite of CHRISTOPH'S assumption that infection by the mycorrhizal fungus takes place only from soil.

A later contribution by RAYNER[11] shows that the endophyte has been isolated and identified as belonging to the genus *Phoma*, and that in association with the heather plants it is able to utilize atmospheric nitrogen. While seedlings of *Calluna vulgaris* seem incapable of growth unless infected soon after germination, the view is expressed that plants would probably grow quite well without mycorrhiza, could seedlings be raised free from infection. In nature the formation of mycorrhiza in all roots is the rule. The development of the endophyte in mycorrhizal cells is markedly inhibited by the low soil temperatures of early spring, and also under experimental culture conditions by sterilized soil and sand cultures. A digestion of the mycelium in the mycorrhizal cells is shown to continue during the growing season, and there seems to be an exchange of nutritive material between the fungus and the vascular plant, with the "balance of profit" on the side of the latter.—GEO. D. FULLER.

Drying timber.—Up to rather recent times, as PATTON[12] points out, air seasoned timber was used in all the best woodwork, but now this method does not supply enough lumber, and some at least must be kiln dried. The research reported on in this paper had for its object the study of the factors involved in

[9] RAYNER, M. CHEVELEY, Mycorrhiza in the Ericaceae. Trans. Brit. Mycol. Soc. **8**:61–66. 1922.

[10] CHRISTOPH, H., Untersuchungen über die mykrophyten Verhältnisse der Ericales und die Keimung von Pirolaceae. Beih. Bot. Centralbl. **38**:115. 1921.

[11] RAYNER, M. CHEVELEY, The nutrition of mycorrhiza plants: *Calluna vulgaris*. Brit. Jour. Exper. Biol. **2**:265–292. 1925.

[12] PATTON, R. T., On the drying of timber. Proc. Roy. Soc. Victoria (N.S. Pt. I) **35**:63–85. 1922.

the drying of timber, and their application to the commercial seasoning of timber. The six factors studied were moisture content, diffusion of moisture, evaporating surface, thickness, humidity, and temperature. Most of the trees studied had a higher moisture content in the sapwood than in the heartwood. The diffusion constant for a number of trees was determined. The oak, for example, has a high moisture content and a low power of diffusion; it is therefore difficult to season. The pine, on the other hand, has a low moisture content and a high power of diffusion; it therefore dries rapidly. Water was lost most rapidly from the transverse surface, that is, in the direction in which the water moves in the tree, and least rapidly from the radial surface; while the loss from the tangential surface was but little more than from the radial. The rate of water loss was independent of the thickness of the block up to a certain point, then, as drying proceeded, the thinner block lost water less rapidly. The influence of different combinations of temperature and moisture were studied. Studies of this kind should result in improved methods of seasoning lumber, especially where kiln drying is the method used.—S. V. EATON.

Virgin forests of Ohio.—In an interesting investigation of the original vegetation of Ohio, SEARS[13] has used as sources of information the records and field notes of the first land surveys of the State, dating back to 1786, county histories, and the journals of travelers. The most abundant trees seem to have been oak, beech, and ash, representing respectively forest associations of (1) *Quercus* and *Carya;* (2) *Fagus grandifolia* and *Acer saccharum* with a sprinkling of *Fraxinus americana* and *Quercus rubra;* and (3) *Fraxinus americana, F. nigra, Ulmus americana,* and *Acer saccharinum.* The distribution of these associations within the glaciated area seems primarily correlated with the system of morainal deposits. Unmixed beech appears to have been limited to the glaciated region, and ash to have been best developed within the Erie plain. Maps present the results of these studies in graphic form.—GEO. D. FULLER.

Classification.—CAMPBELL[14] has made some suggestions in reference to a classification of the plant kingdom "more in harmony with our present knowledge" than "the very antiquated system still in vogue." His suggestions are well worth considering. They involve four primary divisions: Protophyta (including the troublesome Myxomycetes, Flagellates, and Schizophytes), Algae, Fungi, and Embryophyta (Bryophytes, Pteridophytes, and Spermatophytes). It is interesting to note that the four classes of Spermatophytes dispose of the old categories of gymnosperms and angiosperms, being Cycadophyta, Coniferae, Gnetales, and Anthophyta (angiosperms).—J. M. C.

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[13] SEARS, P. B., The natural vegetation of Ohio. I. A map of the virgin forests. Ohio Jour. Sci. **25**:139–149. 1925.

[14] CAMPBELL, D. H., Some suggestions on classification. Science **61**:403–405. 1925.